Short and Long-Term Fitness Consequences of Maternal Care in Wild House Mice *Mus musculus domesticus*

Dissertation
zur
Erlangung der naturwissenschaftlichen Doktorwürde
(Dr. sc. nat.)
vorgelegt der
Mathematisch-naturwissenschaftlichen Fakultät
der
Universität Zürich

Yannick Auclair
aus
Frankreich

Promotionskomitee
Prof. Dr. Barbara König (Vorsitz)
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CONTENTS

The early life is a critical period for an individual as any developmental stress can affect its morphology, physiology, immunology or behaviour. Parental care, which consists in any parental behaviour provided to the offspring after fertilization, is thus essential in species giving birth to offspring that initially cannot thermoregulate or feed by themselves. Although a higher parental investment could improve offspring fitness, parents only have a finite quantity of energy to assign to reproduction. Decisions over energy allocation are particularly important in mammalian species where females are often the only caring parent and where lactation is the most important and costly parental care component to determine offspring development. Moreover, the long period of maternal dependence in this taxon can accentuate the importance of inter-individual variation in maternal care in the short and long term. In this thesis, I investigated the short and long-term fitness consequences of inter-individual variation in maternal care using the house mouse *Mus musculus domesticus* as a study species. House mice are well known for their great adaptability and are therefore a good candidate to examine inter-individual variation. Female house mice provide extensive parental care to their offspring and can be observed nesting solitarily or communally, when females pool their offspring in a single nest where they indiscriminately share all maternal duties.

An observational approach combining social, reproductive and morphological data collected from a wild population allowed me to show that females who nest communally can reduce their maternal load by spending less time in their nest without impairing the amount of maternal attention received by their offspring. Furthermore, I demonstrated that females can confuse the paternity of their litters by pooling them in communal nests which contributes to prevent infanticide and improve offspring survival. A higher maternal investment did not provide returns to females as offspring body mass at weaning failed to predict lifetime reproductive success. Moreover, higher body mass at weaning led to higher adult body mass only in males. Adult body mass, however, did not influence lifetime reproductive success but the heaviest individuals reproduced earlier and lived shorter. The studied population was subject to a strong breeding competition as reflected by the deferred onset of reproduction when population density increased and the skewed reproductive success that was observed in both sexes. Lifetime reproductive success increased with longevity. Males, who lived shorter than females, showed three alternative life history trajectories to maximize their reproductive success whereas only one was followed by females. These life history trajectories were not predicted by body mass or population density, suggesting an influence of other factors like social competence on individuals' lifetime fitness. Finally, I used an experimental approach to test a recent theory suggesting that particular sets of behavioural traits could contribute to

differences in life history traits. To do so, I assessed boldness, exploration, activity, and food consumption in laboratory-born descendants of mice caught from the study population where a survival advantage has been reported in female heterozygous for the *t* haplotype (+/*t*) over homozygous wildtype females (+/+). The longer living +/*t* females, unlike +/+ ones, were less active, slower to form routines and had a lower food consumption. These behavioural traits, which conserve energy and favour cautiousness, may contribute to an extended longevity.

This thesis presents new adaptive hypotheses for the evolution of communal nesting and provides empirical evidence that offspring number should be favoured over offspring quality in the house mouse. Despite a strong breeding competition in which body size plays an important role, other factors like social competence may also have a strong influence on individuals' lifetime fitness in species living in socially complex societies like the house mouse. In line with that hypothesis, this thesis demonstrated that behavioural tendencies can correlate with a life history trait like survival. Whether or not females can tailor the behavioural profile of their offspring through the type of maternal care they provide, however, remains unknown.

Der frühe Lebensabschnitt ist eine kritische Zeit. Jede Form von Stress kann die Morphologie, Physiologie, Immunologie oder das spätere Verhalten eines Individuums beeinflussen. Elterliche Fürsorge, definiert als jegliche elterliche Investition nach der Befruchtung der Eizelle, ist daher von essentieller Bedeutung. Eltern haben nur eine begrenzte Menge an Energie zur Verfügung, welche sie in die Reproduktion investieren können. Entscheidungen darüber, wie diese begrenzte Energie eingesetzt wird, sind besonders wichtig bei Säugetieren. In diesem Taxon sind Weibchen oft das alleinige Elternteil, welche Brutpflege betreiben und die Kosten daher alleine tragen. Laktation ist dabei die wichtigste und kostspieligste Komponente der mütterlichen Fürsorge und hat einen grossen Einfluss auf die Entwicklung der Jungtiere. Ausserdem sind Jungtiere in diesem Taxon oft sehr lange abhängig von ihren Müttern, wodurch individuellen Unterschieden mütterlicher Investition eine noch grössere Bedeutung zukommt. In Rahmen dieser Dissertation untersuchte ich die kurz- und langfristigen Fitnesskonsequenzen von individueller Variation in mütterlicher Fürsorge in der westeuropäischen Hausmaus *Mus musculus domesticus*. Hausmäuse sind bekannt für ihre Anpassungsfähigkeit und daher eine ideale Art um den Effekt individueller Unterschiede zu untersuchen. Neugeborene sind vollkommen hilflos und auf Unterstützung angewiesen (Laktation, Thermoregulation, Schutz). Hausmäuse haben zwei unterschiedliche Strategien für die Jungenaufzucht; Entweder alleine, oder aber zusammen mit einem oder mehreren anderen Weibchen. Bei der gemeinschaftlichen Jungenaufzucht ziehen alle Weibchen ihre Jungtiere in einem Nest gross und teilen sich die mütterlichen Aufwendungen.

Eine empirische Herangehensweise, welche Daten über das Sozialverhalten, die Reproduktion und über die Morphologie kombiniert, ermöglichte es mir aufzuzeigen, dass gemeinschaftlich aufziehende Weibchen die Belastung reduzieren können. Sie verbringen weniger Zeit im Nest, ohne dass dabei ihre Jungtiere häufiger alleine sind. Des Weiteren konnte ich zeigen, dass Weibchen die Vaterschaft ihrer Jungtiere verschleiern indem sie ihre Würfe mit denen anderer Weibchen kombinieren. Diese Verschleierung der Vaterschaft reduziert Infantizid durch männliche Hausmäuse und erhöht damit die Überlebenswahrscheinlichkeit der Jungtiere. Das Körpergewicht der Jungtiere zum Zeitpunkt der Entwöhnung hatte keinen Einfluss auf deren Reproduktionserfolg. Ein direkter Zusammenhang zwischen mütterlicher Fürsorge und Fitness der Jungtiere konnte daher nicht aufgezeigt werden. Das Körpergewicht der Jungtiere bei der Entwöhnung korrelierte nur bei Männchen mit dem späteren Gewicht als adulte Tiere. Das Gewicht der adulten Tiere hatte seinerseits wiederum keinen Einfluss auf den Fortpflanzungserfolg, allerdings reproduzierten die schwersten Männchen früher und hatten eine verkürzte Lebenserwartung. Sowohl

Weibchen als auch Männchen konkurrieren stark untereinander um Fortpflanzung in unserer wilden Population, was sich unter anderem dadurch zeigt, dass mit steigender Populationsdichte das Alter bei der ersten Fortpflanzung steigt und wir in beiden Geschlechtern eine ausgeprägte Variation im Reproduktionserfolg ('reproductive skew') finden. Der Fortpflanzungserfolg auf Lebenszeit korrelierte positiv mit der Lebensdauer. Männchen hatten eine geringere Lebenserwartung als Weibchen und folgten einer von drei verschiedenen „life-history" Strategien um ihre Fitness zu maximieren. Bei Weibchen schien es nur eine Strategie zu geben. Weder das Körpergewicht der Männchen, noch die Populationsdichte beeinflussten welche der drei Strategien ein Männchen verfolgte. Dieses Resultat lässt vermuten, dass andere Faktoren, wie beispielsweise die Sozialkompetenz, einen Einfluss auf den Fortpflanzungserfolg haben können. Ausserdem habe ich eine experimentelle Herangehensweise gewählt um eine neuere Theorie zu überprüfen, welche besagt, dass gewisse Merkmale des Verhaltens zu unterschiedlichen „life-histories" führen können. Ich erhob Daten zur Boldness, zum Erkundungsverhalten, zur Aktivität und zum Futterverbrauch von im Labor geborenen Abkömmlingen unserer Studienpopulation. Ich untersuchte Weibchen die heterozygot sind für den *t* haplotyp (+/*t*) und verglich sie mit wildtyp Weibchen (+/+). +/*t* Weibchen in unserer wilden Population hatten eine höhere Lebenserwartung als ihre +/+ Artgenossen und die im Labor gemessenen Verhaltensweisen zeigen, dass +/*t* Weibchen weniger aktiv waren, länger brauchen um Routinen zu entwickeln und weniger Nahrung zu sich nahmen; alles Dinge welche Energie sparen und deshalb vielleicht zur erhöhten Lebensdauer beitragen.

Diese Dissertation präsentiert neue, adaptive Erklärungen für die Evolution gemeinschaftlicher Jungenaufzucht und liefert empirische Hinweise darauf, dass die Anzahl Junge in Hausmäusen wichtiger ist als deren Qualität. Trotz starker Fortpflanzungskonkurrenz, bei welcher die Körpergrösse eine wichtige Rolle spielt, scheinen andere Faktoren, wie beispielsweise die Sozialkompetenz, in sozial komplexen Arten wie der Hausmaus, von Bedeutung zu sein. Diese Dissertation zeight, dass Verhaltensmuster mit life-history Merkmalen korrelieren können. Inwiefern Weibchen das adulte Verhalten ihrer Jungtiere durch die Art der Brutpflege beeinflussen bleibt für den Moment noch ungeklärt.

Les premiers stades de la vie représentent une période critique pour un individu puisque tout stress développemental peut affecter sa morphologie, son système immunitaire ou son comportement. Les soins parentaux sont essentiels chez les espèces dont les jeunes sont incapables de réguler leur température ou bien de se nourrir par eux-mêmes à la naissance. Bien qu'un investissement parental plus important puisse améliorer l'aptitude phénotypique de la progéniture, les parents ne peuvent allouer qu'une quantité limitée d'énergie aux activités de reproduction. Les décisions d'allocation d'énergie sont particulièrement importantes au sein des espèces mammifères chez qui les femelles sont souvent seules à prodiguer des soins à leur progéniture et où la lactation est la composante la plus importante et la plus coûteuse des soins parentaux déterminant le développement des jeunes. Des différences inter-individuelles dans les soins maternels apportés par les femelles peuvent avoir de larges répercutions grâce à la longue période de dépendance maternelle des jeunes dans ce taxon. Dans cette thèse, je me suis intéressé aux conséquences à court et long terme de la variation inter-individuelle dans les soins maternels sur l'aptitude phénotypique chez la souris domestique *Mus musculus domesticus*. Cette espèce est reconnue pour sa grande adaptabilité et représente par conséquent un candidat idéal pour examiner la variation inter-individuelle. Les femelles prodiguent des soins conséquents à leurs petits et peuvent être observées nichant seules ou dans des nids communautaires lorsque plusieurs femelles regroupent leurs portées dans un seul nid et y partagent tous les soins maternels indistinctement.

Une approche observationnelle combinant des données sociales, d'activité reproductrice et morphologiques collectées dans une population sauvage m'a permis de montrer que les femelles qui avaient élevé leurs petits dans des nids communautaires avaient passé moins de temps dans leur nid sans affecter la quantité d'attention maternelle reçue par les jeunes, réduisant ainsi leur charge maternelle. De plus, j'ai montré que ces femelles pouvaient confondre la paternité de leur progéniture à l'intérieur des nids communautaires ce qui leur a permis de réduire les risque d'infanticides et d'augmenter ainsi les chances de survie de leurs petits. Les femelles n'ont en revanche pas bénéficié d'un retour sur un investissement maternel plus important puisque le poids des petits au sevrage ne prédit pas leur succès reproductif total sur l'ensemble de leur vie. En outre, un poids plus important au sevrage n'a conduit à un poids adulte plus important que chez les mâles. Le poids adulte n'a également pas influencé le succès reproductif total sur l'ensemble de la vie mais les individus les plus lourds étaient plus jeunes à leur première reproduction et ont survécu moins longtemps. La population étudiée était sujette à une forte compétition de reproduction. L'âge à la première reproduction a observé un recul lorsque la densité de population a augmenté et

le succès de reproduction s'est révélé être biaisé à la fois chez les mâles et les femelles. Le succès reproductif total sur l'ensemble de la vie a augmenté avec la longévité. La durée de vie s'est révélée être plus longue chez les femelles que chez les mâles. Alors que trois trajectoires biodémographiques alternatives correspondant chacune à une association particulière entre l'âge à la première reproduction et la longévité ont pu être observées chez les mâles, une seule l'a été chez les femelles. Le recours à l'une ou l'autre de ces trajectoires biodémographiques n'étaient pas prédite par le poids des individus ou la densité de population suggérant l'influence d'autres facteurs comme la compétence sociale sur l'aptitude phénotypique des individus sur l'ensemble de leur vie. Finalement, j'ai utilisé une approche expérimentale pour tester une théorie récente proposant que des ensembles particuliers de traits comportementaux puissent contribuer à l'observation de différences dans les composantes biodémographiques. Pour cela, j'ai mesuré la témérité, la tendance exploratoire, le niveau d'activité, et la consommation de nourriture chez des souris nées au laboratoire mais qui étaient des descendants d'individus capturés dans la population d'étude où un avantage de survie a été rapporté chez les femelles hétérozygotes pour l'haplotype *t* (+/*t*) par rapport à celles homozygotes sauvages (+/+). Les femelles +/*t* à la survie plus longue, contrairement aux +/+, étaient moins actives, plus longues à former des routines et ont consommé moins de nourriture. Ces traits comportementaux qui conservent l'énergie et favorisent la prudence, pourraient contribuer à allonger la durée de vie.

Cette thèse présente, chez la souris domestique, de nouvelles hypothèses adaptatives pour l'évolution de la nidification communautaire et fournit des preuves empiriques que les femelles doivent favoriser le nombre plutôt que la qualité de leur progéniture. En dépit d'une forte compétition de reproduction dans laquelle la taille du corps joue un rôle important, d'autres facteurs tels que la compétence sociale pourraient également avoir une forte influence sur l'aptitude phénotypique des individus sur l'ensemble de leur vie chez les espèces vivant dans des sociétés à l'organisation sociale complexe comme la souris domestique. Conformément à cette hypothèse, cette thèse a démontré que des tendances comportementales pouvaient être corrélées à une composante biodémographique comme la survie. Toutefois, la capacité des femelles à ajuster le profil comportemental de leur progéniture au travers du type de soins maternels qu'elles prodiguent reste inconnue.

GENERAL INTRODUCTION

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Background: The importance of parental care during early life

Offspring that cannot thermoregulate or feed by themselves before reaching weaning age and full independence are at risk of starvation, hypothermia, infanticide or predation whenever unattended by their parents (Galef 1981; Hoogland 1985). Such species therefore show extensive parental care that is required for offspring development and survival to weaning (Clutton-Brock 1991; Galef 1981; Royle, Smiseth & Kölliker 2012).

Parental care consists of any parental behaviour occurring after fertilization, directed at the offspring and likely to improve their lifetime fitness (Royle et al. 2012). Following this definition, parental care includes behaviours such as the choice or construction of a nest or a burrow as well as its maintenance, offspring attendance and protection, and food provisioning (Royle et al. 2012). How much energy the parents should allocate to reproduction to maximize their fitness remains a long-standing question in life history theory (Gittleman & Thompson 1988). Individuals cannot invest indefinitely in their offspring since they only have a finite quantity of energy to assign to reproduction, as suggested by the negative relationship between brood size and offspring quality reported in a wide range of taxa (Charnov & Ernest 2006; Lack 1947; Roff 2002; Stearns 1992).

Any reduction in the amount of care provided by the parents will have, however, a strong impact on the development and future fitness of the offspring (Lindström 1999). The early life is a critical period for an individual as any developmental stress can affect its morphology (Lummaa & Clutton-Brock 2002; Tschirren et al. 2009), physiology (Mirescu, Peters & Gould 2004; Sebaai et al. 2004), immunology (Edwards & Cooper 2005; Prager et al. 2010) or behaviour (Champagne 2010; Laviola & Terranova 1998; Lovic, Gonzalez & Fleming 2001).

In mammals, females are often the only parent caring for the offspring, bearing alone the extensive costs associated with raising offspring. Lactation, which directly influences offspring growth (Gittleman 1985; McDowell, Gates & McDowell 1930), is the most important parental investment component in mammals but the extent to which females can nurse their young is limited by its high energetic costs (Clutton-Brock, Albon & Guinness 1989; Gittleman & Thompson 1988). Lactation represents a large part of a female's energy budget that can reach 70% of her resting metabolic rate at lactation peak when offspring are getting closer to weaning age (Hammond & Diamond 1992; König, Riester & Markl 1988). Females therefore face a trade-off: although they need to forage more to sustain the costs of milk yield (Mann et al. 1983; Myrcha, Ryszkowski & Walkowa 1969), offspring attendance

should not be neglected to avoid hypothermia, starvation or infanticide when conspecifics kill parental care dependent non-offspring (Hausfater & Hrdy 1984).

Such situations are likely to favour the evolution of cooperation over maternal care as it would give females the opportunity to reduce maternal load without diminishing the overall care received by their offspring (West, Griffin & Gardner 2007). Alternatively to reducing their maternal load, cooperating females could increase their benefits by individually investing as much as when alone. Communal care of the offspring, when individuals provide care to all offspring regardless of their affiliation, can be mutually beneficial for all mothers and therefore does not require kinship, even though relatedness may help in stabilizing cooperative interactions (Bshary & Bergmüller 2008; Clutton-Brock 2002). Communal care of the offspring occurs in a wide range of taxa including 15% of all mammalian species (Brown 1978; Gittleman 1985; Riedman 1982). For instance, communal nesting is one form of communal care which is often observed in rodents (Hayes 2000). Communally nesting females typically pool their offspring in a single nest where they indiscriminately share all maternal duties (Hayes 2000). Females have been reported to indiscriminately nurse both offspring and non-offspring in 10% of mammalian species (Packer, Lewis & Pusey 1992).

Although communal nesting has for long been considered as a by-product of social living (Pusey & Packer 1994; but see Weidt, Lindholm & König 2014), there is now increasing evidence that this behaviour is adaptive and can improve offspring survival or growth (Heiderstadt & Blizard 2011; Manning et al. 1995). Females can also benefit from communal nesting as sharing lactation with other females may help to buffer the high energetic costs incurred during the lactation peak whenever litters are not the same age (Godbole et al. 1981; König 2006).

Communal nests also offer a social environment more complex than that of solitary nests as the offspring become exposed to multiple mothers and a larger number of litter mates. Recently, it has been proposed that the amount of social behaviour or maternal care received by the offspring during their early life may tailor their future behavioural tendencies (Branchi et al. 2006; Branchi et al. 2009; Branchi et al. 2013; Kloke et al. 2013; Wu et al. 2013). The concept of animal personality aims at characterising inter-individual differences in behavioural tendencies by looking at behavioural traits that are consistent through time and across situations (David, Auclair & Cézilly 2012; Réale et al. 2007; Réale et al. 2010). Often, these behavioural traits are correlated within or across contexts and are referred to as behavioural syndromes (Bell 2007; David, Auclair & Cézilly 2011; Wilson et al. 2010). “Proactive” individuals, in contrast to “reactive” individuals, have higher activity levels, a

higher metabolic rate, are more exploratory and risk-prone (or bold), and faster to establish routines (Benus et al. 1990; Careau et al. 2008; Careau et al. 2009; Koolhaas et al. 1999; Marchetti & Drent 2000). The recent research on animal personality now investigates its fitness consequences and already reported its influence on life history traits like growth, fecundity and survival (Boon, Réale & Boutin 2008; Both et al. 2005; Stamps 2007).

Aims of research

In my dissertation, I aim to analyse potential fitness consequences of inter-individual variation in maternal behaviour, body mass or personality traits in wild house mice *Mus musculus domesticus*. The great adaptability that allowed house mice to spread all over the world and colonize various types of habitat suggests a wide inter-individual variation (Berry 1970; Berry & Bronson 1992). This social species also presents the advantage of being easy to keep in the laboratory so that both observational and experimental scientific approaches can be conducted (Latham & Mason 2004).

1. Do females benefit from a reduced load of maternal care by nesting communally?

It has recently been shown that female house mice nest communally because of an actual choice and not because of limited opportunities to nest solitarily (Weidt, Hofmann & König 2008; Weidt et al. 2014). The rise and persistence of communal nesting in populations suggests that it can provide females with enough benefits to outweigh its potential costs such as a higher risk of pathogen transmission (Altizer et al. 2003), non-offspring nursing (Packer et al. 1992) or infanticide perpetrated by nesting partners (Hager & Johnstone 2004).

Accordingly, studies have reported that communally-raised offspring benefit from an enhanced thermoregulation (Hayes & Solomon 2006), feeding rate (Jacquot & Vessey 1994; Mennella et al. 1990), growth rate (Heiderstadt & Blizard 2011; Sayler & Salmon 1969, 1971), immuno-competence (Boulinier & Staszewski 2008) and nest defence (Manning et al. 1995) which may all contribute to explaining the higher lifetime reproductive success of communally nesting females compared to solitarily nesting females (König 1994).

The extent to which communal nesting influences females' time budget, however, remains largely unknown. More particularly, there are very few studies that have investigated whether communally nesting females benefit from a reduced nest attendance (Hayes & Solomon 2006; Izquierdo & Lacey 2008). Nonetheless, this particular component of maternal care can be of prime importance through its possible impact on pup survival and females' foraging behaviour and milk yield.

To address the question of whether communally nesting females benefit from a reduced load of maternal care, I compared the time they spend in the nest to that of solitarily nesting females.

A reduced nest attendance would benefit females through increased opportunities to go foraging and sustain milk yield or to protect their territory. However, females' nest attendance may have strong consequences on offspring survival as offspring are highly vulnerable when left unattended by their parents. Although a study reported a higher offspring survival in communal nests compared to solitary nests, the mechanism responsible for that better survival remained unclear (Manning et al. 1995).

2. Do females benefit from an improved offspring survival by nesting communally?

Infanticide, the act of killing conspecific non-offspring before weaning, is reported in a wide range of taxa (Hoogland 1985; vom Saal et al. 1995). Females, who bear extensive costs when their litters are killed, have therefore evolved several strategies to deter infanticide (Agrell, Wolff & Ylönen 1998; Ebensperger 1998). Females can reduce the risk of infanticide through their mating behaviour (Hrdy 1979). Polyandry, when females mate with multiple males, is known to reduce male infanticide (Hosken & Stockley 2003; Parker & Birkhead 2013). By mating with multiple males, polyandrous females give them a possibility of siring offspring that confuses the paternity of the young and inhibits those males from killing what could be their own offspring (van Schaik, Hodges & Nunn 2000; Wolff & MacDonald 2004).

Alternatively, communal nests have been suggested to benefit from an increased nest defence. Similarly to the case in lions *Panthera leo,* a pair of females who conjointly repel infanticidal individuals from their nest could be more efficient than a single female (Packer & Pusey 1983). Although this argument has been used to explain why offspring survival was higher in communal nests compared to solitary nests in the house mouse *Mus musculus domesticus* (Manning et al. 1995), convincing evidence for cooperative female defence of communal nests is still missing. Instead, females could socially obtain the offspring survival benefits associated with paternity confusion by nesting communally. Females who nest communally could pool their litters with those of females that mated with different males to themselves. Singly sired litters could thus be perceived as a large multiply sired litter once together in a communal nest, and infanticide could thereby be reduced for all the litters in the nest.

To test whether females benefit from an improved offspring survival by nesting communally, I examined the relationship between offspring survival and the number of mothers and fathers per nest.

Although females can improve their offspring fitness by nesting communally, their level of maternal investment may also affect offspring fitness. The increased offspring quality at weaning observed whenever offspring received extended maternal care (Dahle & Swenson 2003) suggests that a higher maternal investment could improve offspring lifetime fitness.

3. Do females benefit from weaning heavier offspring?

The importance of maternal investment can be appreciated through maternal effects (Maestripieri & Mateo 2009; Mousseau & Fox 1998; Reinhold 2002). Postnatal maternal effects correspond to the effects of a mother's maternal behaviour on the phenotype of her offspring (Wolf & Wade 2009). In species with a prolonged period of maternal dependence like mammals, the contribution of postnatal maternal effects on offspring body size can outweigh that of prenatal maternal effects (Reinhold 2002; Steiger 2013).

As offspring body mass at weaning correlates with maternal investment (Don Bowen et al. 2001; Falconer 1947; Mateo 2009; McDowell et al. 1930) and as heavier offspring have better fitness expectations (Anderson & Fedak 1985; Festa-Bianchet, Jorgenson & Réale 2000; Klemme, Ylönen & Eccard 2007; Krackow 1993), females have the potential to influence their offspring lifetime fitness through their level of investment.

To address the question of whether females could benefit from weaning heavier offspring, I first quantified the influence of a mother on her offspring body mass at weaning and then tested the influence of offspring body mass on offspring lifetime fitness.

Adult size may be a better predictor of individuals' lifetime fitness as the access to reproduction is restricted to the individuals who achieved the highest ranks along the dominance hierarchy (Rusu & Krackow 2004). Although the largest adults are more likely to become dominant (Clutton-Brock et al. 1979), the social complexity of house mice societies (Latham & Mason 2004; Perony et al. 2012) may allow the rise of different life history trajectories hence explaining inter-individual variation in body mass.

4. What is the influence of adult body mass on life history traits and life history strategies?

An individual's reproductive success is determined by the combination of different life history traits, like the age at sexual maturity or survival, called life history strategies (Stearns 1976). Because of its allometric relationships with several life history traits, body mass is

probably one of the most important factors that influence an individual's reproductive success (Millar & Hickling 1991; Oli & Dobson 2003; Peters 1986).

As large individuals have a physical advantage in aggressive interactions, body mass plays a crucial role in the establishment of dominance hierarchies hence ruling the access to reproduction (Apollonio et al. 1992; Clutton-Brock et al. 1979; Clutton-Brock et al. 1988; Klemme et al. 2007). The onset of reproduction is therefore directly linked to body mass and sex-specific life history strategies may evolve whenever selection pressures on body mass differ between sexes (Clutton-Brock & Guinness 1982). Disruptive selection pressures on body mass can also give rise to alternative life history strategies within one sex (Gross 1996).

Mammalian studies reporting the influence of body mass on life history traits and strategies are unfortunately limited to ungulates that are large, long-lived and slow breeding species (Clutton-Brock & Guinness 1982; Festa-Bianchet et al. 2000; Gaillard et al. 2000; Jorgenson et al. 1993). The majority of mammal species are, however, small, shorter-lived and fast breeders for which lifetime data are still missing.

Here, I tested the influence of adult body mass on life history traits like age at first reproduction, longevity and lifetime reproductive success in a short-lived and fast-breeding species. Furthermore, I also examined what set of these life history traits led to fitness peaks.

Inter-individual differences in fitness may not only be explained by variation in body mass but may also result from particular behavioural tendencies. For instance, life history theory suggests that individuals with different fitness expectations have different behavioural tendencies.

5. Can differences in survival be explained by behavioural tendencies?

Several factors can determine an individual's survival, for example its morphological characteristics (Festa-Bianchet et al. 2000) or the inheritance of an efficient immunity (Lemke, Coutinho & Lange 2004). Recently, behavioural ecologists have proposed that individuals' behavioural tendencies can also have strong fitness consequences (Smith & Blumstein 2008).

The concept of personality, originally used by psychologists in the 1950's, has now been extended to a wide range of taxa from insects to reptiles, fish, birds or mammals and applies to behavioural differences that are consistent through time and across situations (David et al. 2012; Réale et al. 2007; Réale et al. 2010; Wilson et al. 1994). Personality traits like exploratory tendencies, boldness, neophobia or activity are often correlated within or across contexts and are referred to as behavioural syndromes (Bell 2007; David et al. 2011;

Wilson et al. 2010). “Proactive” individuals, in contrast to “reactive” individuals, have higher activity levels and a higher metabolic rate, are more exploratory and risk-prone (or bold), and faster to establish routines (Benus et al. 1990; Careau et al. 2008; Careau et al. 2009; Koolhaas et al. 1999; Marchetti & Drent 2000).

Recent theory combining life history and animal personality suggested that individuals with high expectations of future fitness, who have much to lose and for whom long life is valuable, should be more cautious than individuals with low expectations (Biro & Stamps 2008; Wolf et al. 2007). Thus, long-lived individuals should express a reactive-like personality whereas individuals characterized by a low life expectancy should express a proactive-like personality (Wolf et al. 2007).

In female house mice, a selfish genetic element, the *t* haplotype, has been associated with an increased longevity under natural conditions (Manser et al. 2011). It is possible that the *t* haplotype is associated with behavioural tendencies as it consists of a third of chromosome 17 (Hammerberg & Klein 1975). A gene influencing both male and female mate choice has already been located within the *t* haplotype and genes influencing personality and/or survival, either additively or epistatically or through dominance, could also be located within this region (Lenington 1991).

To test whether survival differences can be explained by behavioural tendencies, I assessed personality traits in mice of both sexes and genetic backgrounds and tested whether +/*t* females, characterized by a high survival rate, express “reactive-like” personality traits and therefore be more shy, less active and less explorative compared to +/+ females, characterized by a lower survival rate.

Study species

The house mouse *Mus musculus domesticus* is a highly territorial small rodent living in socially complex groups (Perony et al. 2012). House mice are plural breeders and the competition over breeding is so high that both sexes have been reported to be infanticidal (McCarthy & vom Saal 1985; vom Saal & Howard 1982). Males fight over territories where they can access and mate with females (DeFries & McClearn 1970; Oakeshott 1974; vom Saal & Howard 1982) while females compete against each other to access the safest nests or shelters (König & Lindholm 2012; Stockley & Bro-Jørgensen 2011; Stockley, Bottell & Hurst 2013; vom Saal et al. 1995). Polyandry is a common reproductive strategy within this species (Dean, Ardlie & Nachman 2006; Firman & Simmons 2008) but females can show preferences for more dominant males or males having a specific genetic background (e.g. wild-type over *t*

haplotype carriers) (Lenington, Coopersmith & Williams 1992). Although mice can reproduce all year, reproductive competition may be more intense in summer than in winter (König & Lindholm 2012). Females give birth to altricial pups that receive maternal care only and remain in the nest until weaning (König & Markl 1987; Latham & Mason 2004). Females are regularly observed sharing a nest with one or more other mothers even though they can rear their pups solitarily (König 1994; Latham & Mason 2004; Weidt et al. 2014). Female house mice also have very limited if any ability to recognize own offspring (Hager & Johnstone 2005; König 1989a, b) so that communally nesting females indiscriminately share all maternal care including nest defence, thermoregulation and nursing of the young (König 1997). Communal nesting in this species is not a by-product of social living as initially suggested (Pusey & Packer 1994) but results from an active social partner choice (Weidt et al. 2014). Moreover, it has been shown that communal nests initiated between females who prefer each other reach a higher reproductive success than those between females who had no preference for each other (Weidt et al. 2008).

Study animals

The data presented in this dissertation were collected from a free-living house mouse population kept in a 70 m^2 former agricultural building in the vicinity of Zurich in Switzerland (König & Lindholm 2012) (Figure 1a). This population has been established in 2002 and numerous persons have compiled an impressive dataset over the years to which I started to contribute in 2008. I took advantage of this long-term dataset in four chapters of my dissertation that were based on these observational data. In addition, one of my chapters followed an empirical approach using laboratory bred descendants from this population.

Although mice can exit the building through several holes in the walls or under the roof, none of the avian or mammalian predators that occur outside can enter. The large permeability of the building towards mice does not allow the collection of emigration data. Food (a 50/50 mixture of oats and hamster food, Landi AG, Switzerland) and water are provided *ad libitum* into 10-12 feeding trays and 15-16 water dispensers to match conditions under which natural house mouse populations are observed (Berry 1970).

Forty nest boxes distributed in the entire building as well as numerous wooden and plastic materials structure the inside to provide territories or shelters to the mice (Figures 1b and 1c). Adult population density is estimated approximately every seven weeks by capturing the entire population and corpses are regularly collected. Every individual weighing at least 18 g is implanted with a subcutaneous transponder (RFID tag; Trovan® ID 100, 0.1 g weight,

11.5 mm length, 2.1 mm diameter) and has an ear tissue sample collected. Each transponder gives a unique identification number to every mouse. The nest boxes allow a close monitoring of reproductive activity. Mice can enter nest boxes through a tube (one per box). Two antennas installed on the entrance tube of all nest boxes continuously record the identity of the mice that enter and leave a nest box.

a. 

b. 

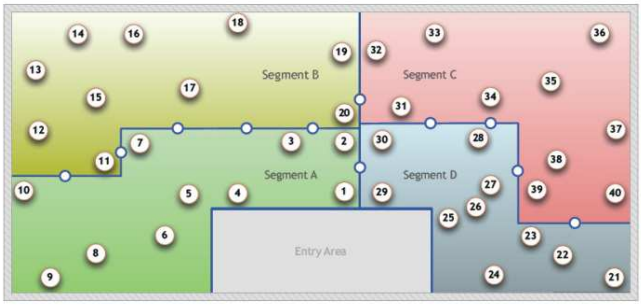
c. 

Figure 1. Pictures of the building from the outside (a), and the inside (b). Forty nest boxes (represented as numbered circles) are equally distributed in the entire area and mice can travel between four segments connected by holes (represented by white circles) (c) (from Leuthold 2009).

The reproductive activity can be monitored by opening the nests from their top, so that litters could be observed. New litters are systematically searched for approximately every ten days, and all litters born are documented. Each new litter is given an identification number, the litter size is recorded, the pups are sexed according to their anogenital distance and genital morphology (Hotchkiss & Vandenbergh 2005), and aged according to morphological development. Skin pigmentation, development of the ears, growth of the fur, teeth eruption, and eye development give reliable cues about the age of the pups (± 1 day, day of birth is considered as day 1) (König & Lindholm 2012) (Figure 2). Every documented litter is

searched for when pups are forecasted to be 13 days old to score survival, take morphological measurements and to collect an ear tissue sample. We consider day 13 as the closest age to weaning that data can be collected because pups start to open their eyes and are mobile at day 14 so they can mix with other litters (actual weaning occurs at 21-23 days old (König & Markl 1987)). Communal litters are defined as those containing pups from more than one mother, which is visually obvious only when pups in the nest differ in age (Figure 3). Therefore, genetic analyses are necessary to confirm maternity.

Figure 2. Age of the pups is determined through their morphological development. The picture shows pups found in a communal nest that have been estimated to be born at a one day interval ranging from 3 to 7 days old (from the left to the right).

a.  b. 

Figure 3. Opening this nest box revealed two mothers providing care to their communal litters (a). Identifying communal litters is obvious when litters differ in age (b).

Thesis outline

Chapter 1 (published in the journal Animal Behaviour) aimed at testing whether communally nesting females could mutually benefit from reduced nest attendance compared to solitarily nesting females. To do so, location data collected from the study population were combined with that of females' reproductive activity. Results showed that communally nesting females spent less time inside their nest than females raising their pups solitarily. Moreover, pups raised in communal nests were left alone for as long as pups raised in solitary nests. Kinship between communally nesting females did not affect the time communal litters were left alone. Communally nesting females therefore have the possibility to allocate more time to foraging or territorial defence without compromising the amount of maternal attention received by their offspring. Moreover, communally nesting females showed some overlap in their stays at the nest that offspring could benefit through more regular meals.

Chapter 2 (accepted in the journal Behavioral Ecology) examined what strategies females could use to deter infanticide, a behaviour which is common in house mice populations. More particularly, the analyses aimed at determining whether communal nesting and polyandry improve offspring survival. Using data from the study population, pup survival was analysed with regard to communal nesting, as measured by multiple maternity, and polyandry, as measured by multiple paternity in solitarily raised litters and in pooled litters of communal nests. Results showed that there were more singly sired litters in communal nests than in solitary nests, and that the majority of them were raised together with litters sired by different males. These litters survived better than singly sired litters raised in solitary nests, and had a survival similar to that of polyandrous litters raised in solitary or communal nests. Singly sired litters could thus be perceived as a large multiply sired litter once together in a communal nest, and infanticide could thereby be reduced for all the litters in the nest. Communal nesting might therefore allow females to socially obtain the offspring survival benefits usually associated with the paternity confusion generated by polyandry.

Chapter 3 (to be submitted) assessed the extent to which females can influence the lifetime fitness of their offspring through their level of maternal investment. In mammals, lactation predicts offspring growth so that offspring body mass at weaning can be used as a proxy for maternal investment. Maternal effects on offspring body mass at weaning and adult body mass were estimated for 384 mice from the study population. Results showed that mothers contributed to 49% and 14% of the variance observed in their offspring body mass at weaning

and once adult, respectively. Then, the influence of offspring body mass at weaning on lifetime fitness was examined. Body mass at weaning only predicted adult body mass in males and had no influence on the onset of reproduction or lifetime reproductive success. The heaviest offspring, however, lived shorter. Moreover, there was a sex difference in survival to the advantage of females. Individuals deferred their first reproduction when population density increased indicating a strong reproductive competition. This study demonstrates that factors influencing offspring reproductive success are independent from body mass at weaning hence from postpartum maternal investment. Females may therefore rather increase offspring number than quality to maximize their own fitness.

Chapter 4 (to be submitted) analysed the influence of adult body mass on life history traits and life history trajectories. Lifetime data from 384 house mice from the study population were used to test the relationship between adult body mass and the age at first reproduction, the number of offspring weaned over a lifetime, and longevity. Furthermore, particular sets of life history traits associated with fitness peaks were identified in each sex. Results showed that body mass did not have any effect on individuals' lifetime reproductive success but the heaviest individuals reproduced earlier and had a shorter lifespan. Concurring with chapter 3, an increase in population density deferred the onset of reproduction, more particularly in males, and females lived longer than males. Lifetime reproductive success, which was highly skewed within each sex, was positively correlated to longevity. Although females showed only one life history trajectory to reach a fitness peak, males followed three alternative life history trajectories to do so. There was no evidence that body mass or population density influenced the life history trajectory followed by individuals. This study suggests that other factors such as social competence may play an important role in an individual's lifetime fitness.

Chapter 5 (published in the journal PLoS ONE) emphasized that behavioural tendencies can also contribute to inter-individual differences in life history traits like survival. To do so, I investigated whether the survival advantage previously observed in female house mice heterozygous for the *t* haplotype (+/*t*) over homozygous wildtype females (+/+) could be explained by reactive-like personality traits that favour cautiousness and energy conservation as suggested by recent theory. Boldness, exploration, and activity were assessed in laboratory-born descendants of mice caught from the study population. Additionally, food consumption was monitored in 48 of these mice. Results showed that +/*t* females, unlike +/+ ones, were

less active, less prone to form an exploratory routine and tended to ingest less food. No similar pattern was observed in males, concurring with the absence of a survival difference between males of different haplotype. This study indicates that longer living house mice express reactive personality traits demonstrating that longevity can correlate with personality, but fails to provide full empirical support for recent theory.

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Nest attendance of lactating females in a wild house mouse population: benefits associated with communal nesting

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Nest attendance of lactating females in a wild house mouse population: benefits associated with communal nesting

Yannick Auclair[1], Barbara König[1], Manuela Ferrari[1], Nicolas Perony[2] & Anna K. Lindholm[1]

[1] Institute of Evolutionary Biology and Environmental Studies, University of Zurich, Winterthurerstrasse 190, CH-8057 Zurich, Switzerland

[2] Chair of Systems Design, ETH Zurich, Weinbergstrasse 56/58, CH-8092 Zurich, Switzerland

Abstract

Among species providing uniparental care, the caring parent faces time constraints and may have to compromise offspring care/protection for self-maintenance. In most mammalian species females raise their offspring without receiving help from males. Communal nesting, when multiple females share a single nest where they rear their pups together, may have evolved as a mutually beneficial cooperative behaviour to reduce mothers' nest attendance without increasing the time their offspring are left alone. We tested this hypothesis using data collected in a free-living house mouse population, *Mus musculus domesticus,* where reproduction occurred in nest boxes and was closely monitored. Individuals were fitted with transponders allowing automatic recording of their location, and a genetic parentage analysis confirmed maternal identity. Compared to mothers raising their pups solitarily, communally nesting mothers spent less time inside their nest. Their pups, however, were left alone for a similar amount of time as solitarily raised pups. The time communal litters were left alone did not covary with the kinship of communally nesting females. These results indicate that communally nesting mothers can allocate more time to foraging or territorial defence without impairing the amount of maternal attention received by their offspring. Nevertheless, communally nesting mothers showed some overlap in their stays at the nest. Offspring may benefit from more regular meals while mothers may gain information on the partner's contribution to combined maternal care which could potentially prevent cheating.

Keywords: Communal nesting – Cooperation – Exploitation – House mice – Infanticide – Kinship – Lactation – Maternal care – Nest attendance – Thermoregulation

Introduction

As altricial offspring are non-mobile and can neither forage nor thermoregulate at birth, extensive parental care is essential to ensure their survival to weaning (Clutton-Brock 1991; Galef 1981). Parents usually keep their offspring inside a protected shelter or nest in which they can influence the inside temperature and avoid access by predators and/or infanticidal individuals (Montgomerie & Weatherhead 1988; vom Saal et al. 1995; Wolff & Peterson 1998). Offspring, however, remain highly vulnerable as they may suffer starvation, low body temperature, infanticide, or predation whenever their parents leave the shelter to satisfy their physiological and/or social needs (e.g. feeding, territory defence) (Galef 1981; Hoogland 1985). How parents respond to these time constraints and allocate their time therefore influences their current and future reproductive success (Stearns 1992).

Although males and females can share parental duties in species providing biparental care, the caring parent in uniparental species may have to compromise offspring care and protection for self-maintenance. Consequently, such species may evolve cooperative strategies in which same-sex individuals associate with each other and share offspring care and defence (West, Griffin & Gardner 2007b). Parental care could be reduced by sharing the parental load with others so that the amount of parental care received by the offspring could remain the same or increase as more individuals care for them (Gittleman 1985; König 1997; Solomon 1991). For instance, if a mother alone cannot attend her nest more than 30% of a day, a perfect alternation and share of the nest attendance with two other mothers could lead to a maternal presence of 90% of a day. Such a mechanism has been suggested to improve offspring survival in communally nesting species (Hayes 2000; König 1997; Wolff & Peterson 1998). Even though kin selection is not necessary for the evolution of such mutually beneficial behaviours (Bshary & Bergmüller 2008; Clutton-Brock 2002), kinship can help in stabilizing the relationship between cooperative partners and thus improves their performance (Holmes & Sherman 1982). Hamilton's rule of inclusive fitness suggests that relatedness between the individuals involved can compensate the extra costs incurred by an individual who has invested in an altruistic behaviour (Hamilton 1964).

Communal nesting, when females rear their offspring in the same nest or shelter, is observed in 15% of mammalian species, a taxon in which parental care consists almost exclusively of maternal care since only the dams contribute to the nutrition of the young to weaning (Hayes 2000; Packer, Lewis & Pusey 1992). Lactating females have to bear high energetic costs that increase with offspring age to reach a lactation peak just before weaning, a situation that increases a mother's need for foraging (Clutton-Brock, Albon & Guinness

1989; Hammond & Diamond 1992). Although communal care can increase the risks of pathogen transmission (Roulin & Heeb 1999) or infanticide (Hager & Johnstone 2004), offspring raised under these conditions can benefit from enhanced thermoregulation (Hayes & Solomon 2006), feeding (Jacquot & Vessey 1994; Mennella et al. 1990), growth rate (Sayler & Salmon 1969, 1971), immuno-competence (Boulinier & Staszewski 2008), and nest defence (Manning et al. 1995). Furthermore, nursing indiscriminately own and other females' offspring when litters are of different ages may help females to reduce peak energy demand by spacing lactation peaks just before weaning (Godbole et al. 1981; König 2006).

In house mice, laboratory experiments have shown that communally nesting females cannot discriminate their own offspring from other females' offspring (König 1989a, b; König 1993; Manning et al. 1995). They also seem unable to control the pups' access to their nipples to prevent milk theft (Packer et al. 1992). Consequently, pups raised in communal nests receive milk from all females (König 2006) which can result in a faster growth rate (Heiderstadt & Blizard 2011; Sayler & Salmon 1969). Communally nesting females, on the other hand, benefit from improved lifetime reproductive success due to higher offspring survival until weaning (König 1994a). Another laboratory study associated communal nesting with a lower risk of infanticide to explain the better offspring survival observed within communally raised litters (Manning et al. 1995). The influence of communal nesting on nest attendance, however, has received very little attention (Hayes & Solomon 2006; Izquierdo & Lacey 2008) despite its potential benefits in improving pup survival.

Data from laboratory experiments may not allow generalisation of any benefit of nest attendance, as the laboratory is a rather luxurious environment (controlled temperature, food and water easily available, rarely if ever territorial competition, etc.) compared to a natural situation. Using data collected from a wild house mouse population we analysed mothers' nest attendance to test whether communal nesting could benefit mothers and/or their pups. Accounting for litter size and pup age, we tested whether communal nesting influenced the amount of time mothers spent in the nest with their litters and the amount of time pups were left alone in the nest by their mother (or mothers for pups raised in communal nests). Furthermore, we looked whether the number of caring mothers and their kinship, as reflected by their coefficient of coancestry, influenced the time offspring were left without maternal attention in communal nests.

Material and methods

Study species

The house mouse, a small rodent living in socially complex groups, is useful for testing the link between communal nesting and nest attendance (König & Lindholm 2012). Female house mice give birth to altricial pups kept in a nest until weaning and which receive maternal care only (König & Markl 1987; Latham & Mason 2004). Females are regularly observed sharing a nest with one or more other mothers even though they can rear their pups solitarily (König 1994a; Latham & Mason 2004; Weidt, Lindholm & König 2014). Familiarity between females has been reported to be as important as genetic relatedness for social partner choice (König 1994b; Weidt, Hofmann & König 2008). Competition over reproduction is high in this plurally breeding species (König & Lindholm 2012) and both sexes can be infanticidal (McCarthy & vom Saal 1985; vom Saal & Howard 1982). Nest attendance could therefore play an important role in reproductive success through an increase in the amount of care the offspring receive or through a better protection of the nest against intruders (Lewis & Pusey 1997).

Study population

Data were collected from an open free-living house mouse population in a 70 m^2 building, open to dispersal but closed to predators, in the vicinity of Zurich, Switzerland. Numerous wooden and plastic materials structured the inside of the building to provide territories or shelters to the mice. Food (a 50/50 mixture of oats and hamster food, Landi AG, Switzerland) and water were provided *ad libitum* into ten feeding trays and 15 water dispensers.

Every seven weeks, all individuals of the population (during the two year study period: 146 ± 7 adult mice and 57 ± 11 subadults [mean ± SE]) were captured within a day between 10:00 and 18:00. To that end, experimenters encouraged mice previously spotted in shelters or refuges to leave their hiding place (by blowing air, making some noise or gentle shakes when necessary) and head towards a glass jar in which they are captured and weighed. As mice prefer walking along edges and cover their territory following the same routes, it is possible to predict their preferred paths in a structured area like the inside of the building. A mouse moving from a shelter to another will therefore enter a glass jar placed on one of these well-used runs.

Every individual weighing at least 18 g was implanted with a subcutaneous transponder (RFID tag; Trovan® ID-100A implantable microtransponder: 0.1 g weight, 11.5 mm length, 2.1 mm diameter; implanter Trovan® IID100E; Euro ID Identifikationssysteme

GmbH & Co, Germany) in the scruff of its neck and had an ear tissue sample collected (ear puncher Napox KN-293: 1.5 mm diameter) while being handled with a one-hand restraining technique. Each transponder gave a unique identification number to every mouse and allowed a non-invasive recording of their location (König & Lindholm 2012; Perony et al. 2012; Weidt et al. 2008). No obvious adverse effects of these transponders on the behaviour or physiology of the mice have ever been observed in this population or reported in the literature. Ear tissue samples have been used as genetic material as recommended by the Swiss Federal Law on Animal Protection.

The whole procedure was performed by a trained and licensed animal care technician (FELASA-Category A) and lasted no longer than 3 minutes per mouse before being released. Neither analgesic nor anaesthetic were used as they would prolong the duration of this rapid procedure and induce more stress. No bleeding or infection of the transponder implantation site has been observed and there was no evidence that transponders migrated around the body. In the meantime, litters were processed by Y.A., B.K. or A.K.L. (FELASA-Category C; see "*Reproductive Activity*" section) so that they were not at risk of infanticide while mothers were handled. More information about the set-up and population can be found in König and Lindholm (2012). Data collection was approved by the Veterinary Office Zurich, Switzerland (Kantonales Veterinäramt Zürich, no. 215/2006).

Reproductive activity

Forty nest boxes distributed in the entire building allowed a close monitoring of reproductive activity. Mice could enter nest boxes through a tube (one per box). Two antennas installed on the entrance tube of all nest boxes continuously recorded the identity of the mice that entered and left a nest box, allowing calculation of the duration of their stays (in seconds). Experimenters could open the nests from the top, so that litters could be observed, and pups could be counted and aged. We searched for new litters approximately every ten days, and all litters born between January 2008 and December 2009 were documented. Litter size was recorded and pup age was estimated based on morphological development. Pigmentation of the skin, development of the ears, fur growth, teeth eruption, and eye development give reliable cues about the age of the pups (± 1 day). Every documented litter was searched for to collect an ear tissue sample when pups were forecast to be 13 days old. We consider day 13 as the closest age to weaning that data can be collected because pups start to open their eyes and are mobile at day 14 so they can mix with other litters (weaning begins at 17 days and is terminated at 21-23 days old (König & Markl 1987)).

Genetic & maternity analyses

We extracted DNA from the ear tissue samples collected on all adults captured and all pups sampled at their 13th day to determine maternity. We isolated DNA using salt-chloroform extraction (Müllenbach 1989). Twenty-five microsatellite loci were amplified in four multiplex PCR reactions (Chr1_20, D2Mit145, D3Mit278, D4Mit227, Chr5_20, D5Mit122, D5Mit352, D6Mit139, D6Mit390, D7Mit17, D7Mit319, Chr8_3, D8Mit115, D9Mit201, Chr10_11, D10Mit230, D11Mit150, D11Mit90, Chr12_2, D12Mit91, D13Mit88, D14Mit44, D16Mit139, D18Mit194, and Chr19_17). Marker information is available in Schimenti & Hammer (1990), Meagher & Potts (1997), Bult et al. (2008), Teschke et al. (2008), and Hardoin et al. (2010). PCR reactions used the Qiagen Multiplex PCR Kit or AmpliTaq Gold DNA Polymerase (Applied Biosystems) and a final concentration of 0.075 – 0.4 µM primer for 28 - 31 cycles using a 60°C annealing temperature. We analysed PCR products using a 3730xl DNA Analyzer (Applied Biosystems) and Genemapper software (Applied Biosystems). There were no significant deviations from Hardy-Weinberg equilibrium (χ^2_{50} = 62.77, $P > 0.160$) for the 25 loci in testing all adult and subadult mice ($N = 55$) that were present in the barn at a reference time point, using Genepop on the Web (Raymond & Rousset 1995; Rousset 2008).

Maternity analyses were conducted for pups born in 2008 – 2009 using CERVUS 3.0 (Kalinowski, Taper & Marshall 2007). For each pup, candidate mothers were considered to be those females that were present in the barn within two days of the estimated pup birth date. The list of candidate mothers per pup included on average 78 females for 2008 and 103 females for 2009. We used an error rate of 0.01 in CERVUS analyses based on the frequency of alleles scored differently between PCR amplifications of 100 individuals on average per locus, which was 0.006. The proportion of loci typed was 0.99. We considered 100,000 offspring and a sampling rate of 90% of mothers for simulations to generate critical delta values. Maternity assignments were accepted at a 95% level of confidence and only when no more than one mismatching allele occurred between putative mother and offspring. Over the two years, success at assigning mothers was 87 - 88%. However, as a 95% level of confidence population-wide can still sometimes lead to assignment errors (Walling et al. 2010), we adopted a conservative approach and excluded from the data set any litters of size one as they may not provide enough information to ensure a reliable maternity assignment. In this population the average litter size at birth is 5.5 whereas litter size at 13 days of age is four giving an average loss of 0.14 pups per day (Manser et al. 2011).

Kinship between communally nesting mothers

Kinship between communally nesting mothers was assessed by the coefficient of coancestry, which is the probability that an allele randomly chosen from one individual is identical by descent to an allele randomly drawn from the same locus of another individual (Malécot 1948). We assessed kinship between two mothers nesting communally by the Malécot coancestry coefficient using the software *Pedigree Viewer* (version 6.5b, http://www-personal.une.edu.au/~bkinghor/). Whenever a communal nest involved more than two mothers we averaged the different pairwise coancestry coefficients. The average kinship between communally nesting females was 0.16 ± 0.03 and ranged from 0 to 0.54.

Communal versus solitary nesting

Communal nests were defined as those containing litters produced by more than one mother. As communal nests are easy to identify only when they contain litters of different age, genetic analyses confirmed maternity of each pup. Note that our study was based on an observational design so that females were not manipulated and free to choose whether to breed communally or solitary.

Variables measured

For every documented litter, presence of adults in the nest was recorded by the antenna system for a tracking period starting from the first time the litter was found and ending when pups were 13 days old. During this period the antenna data allowed us to measure the cumulated time a mother spent with her litter as well as the frequency of her visits. We divided the cumulated time spent in the nest by the total number of visits to calculate the average duration of a visit to the nest. Moreover, we calculated the cumulated time a litter was neither with its mother nor with the mother of its litter mates when raised in a communal nest.

Data refinement

One hundred and fourteen litters in which there was no change in rearing conditions (communal or solitary nesting) were used in the analyses. Of those, 42 litters were excluded since only one day of tracking was available (otherwise, tracking period ranged from 3 to 13 days). Tracking is imprecise if females move their litter to another nest box. Since females sometimes move litters between nest boxes after disturbances, we refrained from inspecting nests before litters were 13 days old. Nevertheless, to make sure that we only considered

litters which remained in the same nest box during the tracking period, we excluded litters for which the proportion of time the mothers spent in the nest with their offspring in relation to the total time they spent in all nest boxes during the tracking period was lower than an arbitrary cut-off of 30%. In the laboratory, females spend more than half of their time in the same cage as their offspring (König & Markl 1987). After this refinement which excluded another 21 litters, the final range of the time females spent in the same box as their pups ranged from 47.4% to 100.0% (N = 51 litters).

This study presents data from 24 communal litters and 27 solitary litters, produced by 51 mothers between January 2008 and December 2009. Communal litters were older (average pup age over the tracking period) (t_{49} = 2.32, P = 0.025) and smaller (t_{49} = -4.26, P < 0.001) than solitary litters (Table 1). Both communal and solitary litters were tracked for a similar period (t_{49} = -1.68, P = 0.099; communal: 7.9 ± 0.5 days, solitary: 9.1 ± 0.5 days). The whole antenna data set is available to download in open access format as Supplementary Material of Perony et al. (2012).

Table 1. Summary of the raw data observed for communally and solitarily nesting mothers.

	Solitarily nesting mother		Communally nesting mother	
	Mean	± *SE*	*Mean*	± *SE*
Number of mothers	1.0	0.0	2.2	0.1
Litter size	5.5	0.3	3.7	0.3
Litter age (averaged over the tracking period, in days)	8.8	0.3	10.0	0.4
Cumulated time in the nest (sec/day)	31343.9	2400.9	25160.4	2809.2
Number of visits to the nest (per day)	15.2	2.6	12.3	1.8
Duration of a visit to the nest (sec)	3251.9	463.6	2508.4	239.2
Time spent alone by the litters (sec/day)	55056.1	2400.9	42400.6	4095.8

Statistical analyses

Statistical tests were carried out using R 2.15.0 (R Development Core Team 2012). We followed a proportion data analysis procedure to analyse the cumulated time the mothers spent in their nest and the cumulated time the pups were left alone by the mothers in their nest (both in seconds) using independent generalised linear models fitted by a quasi-binomial error distribution (Crawley 2007). Pup age, litter size, communal nesting (yes or no), and their second-degree interactions were used as predictors. Using the same effects structure, the frequency of mothers' visits (log-transformed to satisfy linearity) and their average duration were analysed with two independent linear models. We also used a generalised linear model fitted by a quasi-binomial error distribution to test the influence of the number of mothers,

their kinship, pup age, number of pups in the nest, and their second degree interactions on the time spent alone by pups raised in communal nests. The significance of the predictor variables in the models was assessed using F-tests.

Results

Lactating female house mice spent a considerable amount of their time in the nest with their pups (36% when rearing litters solitarily, and 29% when rearing litters communally; Table 1). The frequency of a mother's visit to her litter was not influenced by pup age, litter size, communal nesting, or any of their interactions (Table 2). Furthermore, communally nesting mothers made significantly shorter visits to their litters than solitarily nesting mothers (Table 2; Figure 1a). The duration of a mother's visit was not influenced by pup age, litter size or any of the interactions involving pup age, litter size and communal nesting (Table 2).

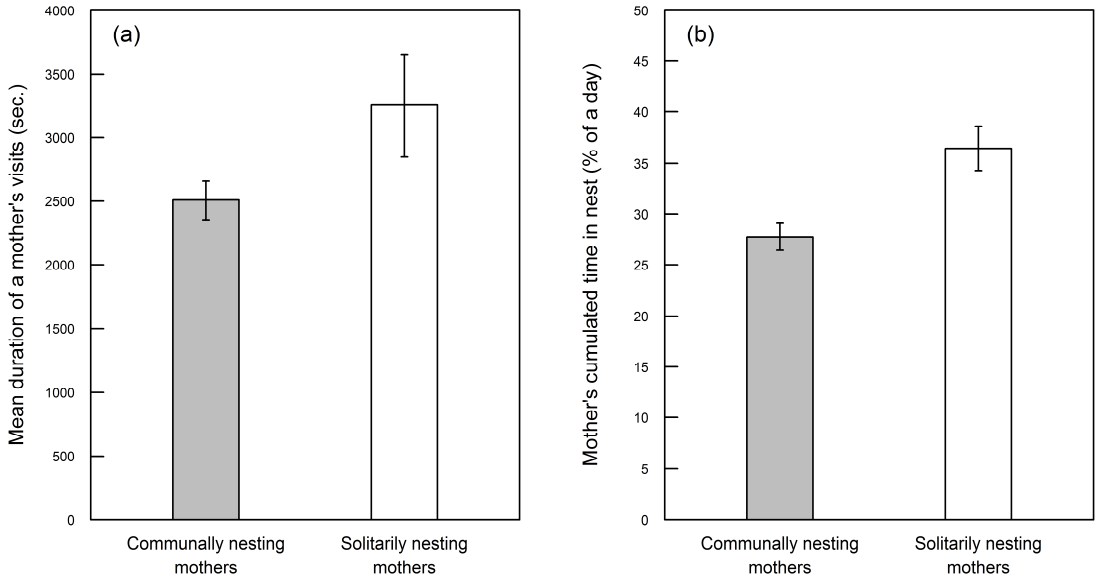

Figure 1. Mother's nest attendance represented as (a) the average duration of her visits and (b) the cumulated time she spent in her nest over a day. Figure shows model predictions ± 95% CI.

Although the cumulated time a mother attended her nest was not significantly influenced by pup age or litter size, solitarily nesting mothers spent significantly more time inside the nest with their litters than communally nesting mothers (Table 2; Figure 1b). None of the interactions between pup age, litter size and communal nesting had a significant influence on a mother's nest attendance (Table 2).

The amount of time litters were left alone by their mother, and the mothers of the other litters for those raised in communal nests, was not influenced by litter size, communal nesting

or their interaction (Table 2). However, older litters spent less time alone in their nest than younger ones; the negative relationship between pup age and the time left alone was stronger for litters raised in communal nests than for those raised in solitary nests (Table 2; Figure 2). The interaction between pup age and litter size had no significant effect on the amount of time litters were left alone (Table 2).

Table 2. Results from multivariate linear or generalised linear models (when appropriate) explaining variation in the frequency and duration of a mother's visit to her litter as well as in a mother's cumulated time in her nest and the cumulated time litters were left alone.

	Frequency of a mother's visit		Duration of a mother's visit		Mother's cumulated time in nest		Cumulated time litters were alone	
	$F_{1.50}$	P	$F_{1.50}$	P	$F_{1,50}$	P	$F_{1.50}$	P
Pup age	0.03	0.862	0.33	0.570	0.45	0.503	**17.03**	**< 0.001**
Litter size	0.84	0.363	2.11	0.153	0.21	0.651	1.63	0.209
Communal nesting	0.01	0.976	**5.28**	**0.026**	**8.04**	**0.007**	1.40	0.242
Litter size : Pup age	1.01	0.320	2.46	0.124	0.94	0.338	0.01	0.990
Communal nesting : Pup age	1.71	0.197	0.02	0.886	2.99	0.091	**21.51**	**< 0.001**
Communal nesting : Litter size	0.65	0.426	1.53	0.223	0.15	0.698	1.63	0.208

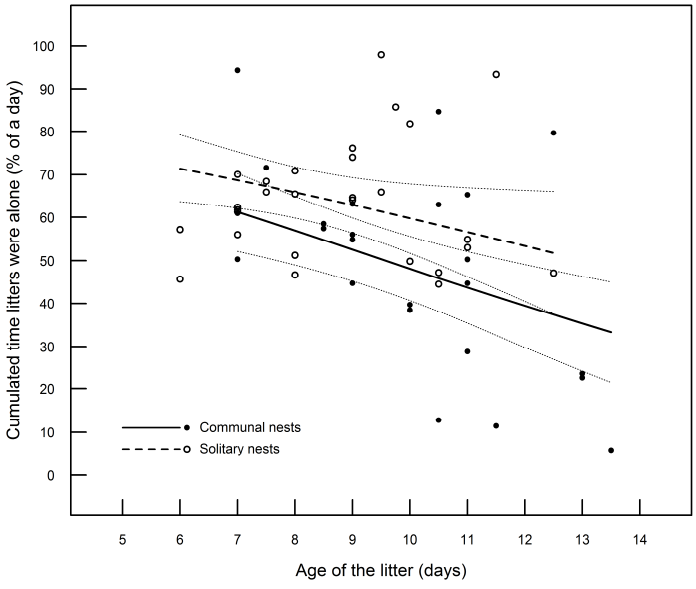

Figure 2. Proportion of a day litters were left alone with regard to their age and solitary or communal nesting. Figure shows model predictions ± 95% CI.

Within communal nests, the time litters were left alone was not significantly influenced by the number of caring mothers ($F_{1,21}$ = 0.17, P = 0.687), their kinship ($F_{1,21}$ = 0.52, P = 0.479), pup age ($F_{1,21}$ = 3.42, P = 0.082) or the number of pups ($F_{1,21}$ = 0.11,

$P = 0.748$). None of the second degree interactions were significant ($P > 0.05$). Moreover, the cumulated time per day communally nesting females spent in the nest was not related to the ratio of own offspring to total offspring in a communal nest (Pearson's correlation: $r = 0.11$, $N = 24$, $P = 0.617$).

Discussion

The present study shows that communally nesting mothers spent less time attending their litters than solitarily nesting mothers in a wild population. Although communally nesting mothers visited their nest as often as solitarily nesting mothers, they made shorter visits to them. This saving in time at the nest indicates that mothers may mutually benefit from communal nesting. A reduced nest attendance gives lactating mothers the opportunity to spend more time foraging which is necessary to increase milk yield or quality (Kretzmann et al. 1991; Mann et al. 1983; Myrcha, Ryszkowski & Walkowa 1969), or to reduce opportunity costs by engaging in other activities like patrolling the territory to refresh urine markings or repel potentially infanticidal individuals (Hurst 1990; Latham & Mason 2004). To analyse the foraging hypothesis further it would be interesting to equip access to feeding trays with antennas and thus quantify time spent feeding. Such a method should allow testing of whether foraging behaviour covaries with nest attendance.

Since our study is based on an observational design, the differences in nest attendance observed among communally nesting females could be confounded by other factors. House mice descended from the same population have been shown to express consistent inter-individual differences in their behaviour (Auclair, König & Lindholm 2013). The differences in nest attendance between solitarily and communally nesting females might thus be driven by their predisposition to associate with individuals of similar behavioural profiles. Such a scenario, however, is not very likely as a recent study reported that female house mice do not follow a unique reproductive strategy, solitary or communal nesting, over their lifetime but can switch between reproductive events (Weidt et al. 2014).

Mothers increased the time spent in the nest with increasing age of their offspring. Because offspring have higher energetic requirements when approaching weaning age, increasing time in the nest may reflect increasing maternal care. This effect was more pronounced in communally nursed litters. Nevertheless, as mentioned before, mothers raising offspring communally were generally more often absent from their nest (on average 71% of a day; Table 1) than solitarily nesting mothers (64%), suggesting that solitarily nursing mothers are constrained in efficient milk investment or in gaining benefits from spending time outside

of the nest (Kenagy et al. 1990; König & Markl 1987; König, Riester & Markl 1988; Millar 1977; Priestnall 1972). Furthermore, in agreement with previous reports of the inability of females to recognize their own offspring (König 1989a, b; König 1993; Manning et al. 1995), the nest attendance of communally nesting females did not covary with their relative contribution to the amount of pups pooled in communal nests.

As females nesting communally spent 29% of a day in their nest (Table 1), one could predict that if two females sharing a communal nest (which was the case in the majority of the communal nests observed, Table 1) alternate their stays at the nest, and never meet, their litters should be attended for a total of 58% of a day. Communally raised litters were, however, attended for 51% of a day (litters were left alone for 49% of a day; Table 1). As a consequence, communally nesting females do show some overlap, since each mother stays in the nest for longer than 50% of the time the pups were attended. Overlap in the presence of mothers at the nest has been reported in two cases of communally nesting meadow voles *Microtus pennsylvanicus* (McShea & Madison 1984). Further studies will have to reveal whether communally nesting females influence each other's presence in the nest or whether they overlap according to random expectation.

Our observation that communally nursing females made shorter visits to their litters suggests that they can leave the nest earlier than solitarily nursing females after a nursing bout. In the laboratory, a nursing bout lasts approximately 20 minutes and does not differ between communally and solitarily nursing females (König & Markl 1987; König 1993). Solitary females in the wild population may have to stay in the nest to warm the litters after a nursing bout. In communally nesting females, in contrast, the short overlaps in their stays may allow them to leave the nest shortly after the completion of a nursing bout as their cooperative partner can ensure the warming of the litters and even initiate another nursing bout. Offspring may thus further benefit from shortened meal intervals (Caraco & Brown 1986).

For the mothers, on the other hand, such overlap could provide information on the partner's contribution to combined maternal care which could potentially prevent cheating. The presence of an audience or cues suggesting their presence is known to encourage cooperation (Bateson, Nettle & Roberts 2006; Pinto et al. 2011). Information on the partner's investment into the combined litters may also be communicated by the sucking behaviour of pups, reflecting whether they had been nursed during a female's absence from the nest. Cooperation and competition are often closely linked, and cheaters can greatly improve their immediate pay-off by cooperating less than a fair share with their partners (West, Griffin & Gardner 2007a). Individuals initiating cooperative behaviours are always susceptible to

exploitation by others, as shown in a wide range of taxa from bacteria to fish, birds, and mammals (Andersson & Eriksson 1982; Bshary & Grutter 2002; Nowak 2006; Velicer & Vos 2009). A lower than proportional share of nursing would allow a female to lower the large energy expenditure usually associated with lactation (Hammond & Diamond 1992). Furthermore, it has been shown that the litter of the first female to give birth in communal nests is more susceptible to infanticide (Andersson & Eriksson 1982; Koenig et al. 1995; König 1994a). An infanticidal second female would increase the ratio of own to total offspring in the communal nest. Such conflicts are likely to occur between females initiating a communal nest right after litters are born which may explain why communally raised litters were smaller than those raised solitarily when we found them.

The time communal litters were left alone was apparently not influenced by their kinship. Mutually beneficial behaviours can occur without kinship (Bshary & Bergmüller 2008; Clutton-Brock 2002). Unrelated females have been reported to protect other females' offspring in other mammalian species such as sperm whales (*Physeter macrocephalus*) and African elephants (*Loxodonta africana*) (Lee 1987; Whitehead 1996). Female wild house mice also successfully communally nurse with unrelated females under laboratory conditions, when given the opportunity to choose among social partners (Weidt et al. 2008).

Our study reports that communally nesting mothers reduce their nest attendance compared to solitarily nesting females. This suggests that communally nesting mothers can allocate more time to foraging to face the energetic burden of lactation, or to protect the territory and nest against intraspecific competitors. Moreover, the amount of maternal attention received by offspring raised in communal nests was even higher, at least for older pups, than that of offspring raised in solitary nests. Nevertheless, communally nesting mothers showed some overlap in nest attendance. Such behaviour may perhaps prevent a reduction in contribution to maternal care by nesting partners. The extent to which communally nesting females exploit each other remains unknown and requires more investigation.

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Socially mediated polyandry:
a new benefit of communal nesting in mammals

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Socially mediated polyandry: a new benefit of communal nesting in mammals

Yannick Auclair, Barbara König & Anna K. Lindholm

Institute of Evolutionary Biology and Environmental Studies, University of Zurich, Winterthurerstrasse 190, CH-8057 Zurich, Switzerland

Abstract

In many species, females have evolved behavioural strategies to reduce the risk of infanticide. For instance, polyandry can create paternity confusion that inhibits males from killing offspring they could have sired. Here, we propose that females could socially obtain the same benefits by nesting communally. Singly-sired litters could be perceived as a large multiply-sired litter once pooled together in a single nest. Long-term data from a wild house mouse population showed that monandrous litters (singly-sired) were more common in communal than in solitary nests and 85% of them were raised with litters sired by different males hence becoming effectively polyandrous (multiply-sired). These socially polyandrous litters had significantly higher offspring survival than genetically or socially monandrous litters and reached a similar survival to that of multiply-sired litters raised in solitary or communal nests. Furthermore, the number of sires within nests significantly improved offspring survival whereas the number of mothers did not. These results suggest that the survival benefits associated with communal nesting are driven by polyandry and not communal defence. This socially mediated polyandry was as efficient as multiple paternity in preventing infanticide, and may also occur in other infanticidal and polytocous species where the caring parent exhibits social behaviour.

Keywords: Cooperation – Communal nesting – Maternal defence – Multiple mating – Mammals – *Mus musculus domesticus*

Introduction

Infanticide, the act of killing parental care dependent conspecific non-offspring, is reported in a wide range of taxa, and is perpetrated by both males and females (Hausfater & Hrdy 1984; Hoogland 1985). For the perpetrator, infanticide may be accidental (e.g. offspring crushed by fighting adults), provide food resources, reduce resource competition, reduce future competitors of own offspring, prevent adoption or, for males, potentially reduce other males' reproductive success while increasing and hastening their access to victimized females (Ebensperger 1998). Females typically bear extensive reproductive costs compared to males, and thus are likely to have evolved several counter-strategies to minimise loss of reproductive investment (Agrell, Wolff & Ylönen 1998).

Females can reduce infanticide by their mating behaviour through polyandry, by mating with multiple partners during a single reproductive event (Hrdy 1979). Polyandry can provide females with access to resources and indirect (genetic) fitness benefits (Hosken & Stockley 2003; Parker & Birkhead 2013), but may also reduce the vulnerability of offspring to infanticidal males. Polyandrous females give multiple males a perceived reproductive contribution, which creates paternity confusion that inhibits those males from killing what could be their own offspring (van Schaik, Hodges & Nunn 2000; Wolff & MacDonald 2004). In the bank vole *Myodes glareolus,* a species in which females do not gain resources from males and in which infanticide is a heritable strategy (Mappes 2012), recent experiments showed that recruitment was improved when females mated multiply with all resident males compared to multiple matings that included only one resident male (Klemme & Ylönen 2010).

An alternative route for females to reduce infanticide is to prevent conspecifics that represent a threat from accessing their offspring through increased nest defence (Agrell et al. 1998). However, survival and social constraints (e.g. searching for food, territory defence) can limit the time that females can spend on nest defence. Consequently, females might engage in a cooperative strategy and nest communally, allowing offspring defence duties to be shared and potentially reducing the time the young are left alone. Cooperative interactions of that kind do not require kinship between the partners to evolve, although it may favour more stable relationships, as they are mutually beneficial (Bshary & Bergmüller 2008; Clutton-Brock 2002). For instance, in lions *Panthera leo* unrelated females form coalitions that are more successful in protecting offspring than a single female alone (Packer & Pusey 1983). Similarly, an increased nest defence has been suggested to explain why communally nesting female house mice *Mus musculus domesticus* benefit from higher rates of offspring survival

compared to solitarily nesting females who raise their litters alone (Manning et al. 1995). Convincing evidence for cooperative female defence of communal nests, however, is still missing in this species.

In the present study, we propose a novel hypothesis to explain why offspring survival is higher in communal nests. Communal nesting allows females to pool their litters in a nest with those of females that mated with different males. Singly sired litters could thus be perceived as a large multiply sired litter once together in a communal nest, and infanticide could thereby be reduced for all the litters in the nest. We therefore tested the hypothesis that communal nesting allows females to socially obtain the offspring survival benefits associated with paternity confusion. To that end, we used long-term data from a free-roaming population of wild house mice *Mus musculus domesticus*.

The house mouse is a highly territorial species where reproductive competition is pronounced (König & Lindholm 2012; Oakeshott 1974) and favours infanticide (vom Saal et al. 1995). Females are known to raise their litters solitarily or communally by grouping their pups in a single nest (Weidt, Lindholm & König 2014) in which they share maternal care (König 1997). Polyandry is a common reproductive strategy within this species that results in multiply sired litters (Dean, Ardlie & Nachman 2006; Firman & Simmons 2008; Manser et al. 2011) but its influence on infanticide is currently unknown. We measured polyandry through multiple paternity in solitarily reared litters or in the pooled litters from communal nests, and communal nesting through multiple maternity of pooled littermates. Then, we tested whether polyandry and communal nesting improved offspring survival. We accounted for population density as a predictor of the intensity of the intra-sexual reproductive competition, a factor that can favour infanticide (Ebensperger 1998; Mappes 2012).

Material and methods

Study population and reproductive activity

Data were collected from a wild house mouse population open to dispersal but closed to predators established in a 70 m^2 former agricultural building outside of Zurich, Switzerland (König & Lindholm 2012). Mice are subject to predation from cats, foxes, and birds of prey when they leave the building. Food, a 50/50 mixture of oats and hamster food (Landi AG, Switzerland), and water were provided *ad libitum* to avoid enhancing infanticide (Mappes 2012). This set-up represents a natural habitat for mice, a species which is commensal with humans and establishes populations where there is easily accessible food (Berry 1970; Cucchi et al. 2002; Pocock, Searle & White 2004). Adult population density was estimated every

seven weeks by capturing the entire population. Matings cannot be controlled in this population as it would require removing individuals from their territories to laboratory conditions. Females and males were therefore free to choose their mating partner(s) and females could choose to nest solitarily or communally. Reproduction occurred in 40 nest boxes in which we systematically searched for new litters approximately every 10 days from January 2007 to December 2009. All litters were documented, and pup age was estimated based on morphological development. Skin pigmentation, development of the ears, growth of the fur, teeth eruption, and eye development give reliable cues about the age of the pups (± 1 day, day of birth was considered as day 1) (König & Lindholm 2012). This study includes litters found in the first three days of life. Animal use and experimental design were approved by the Veterinary Office Zürich, Switzerland (Kantonales Veterinäramt Zürich, no. 215/2006).

Pup survival

We searched intensively for every documented litter when the pups were expected to be 13 days old and used survival to 13 days as a proxy for survival until the onset of weaning. Although weaning starts at 17 days (König & Markl 1987), 13 days old is the closest age to weaning we can handle litters without disturbance as pups open their eyes and become mobile at 14 days old (König & Lindholm 2012). Pup survival was defined by the difference in litter size between the first (age 1-3 days) and second census (age 13 days). Pups that were missing at the second census were considered deceased. Previous studies have reported that pups killed by infanticide typically present bites on their head, neck or stomach or miss body parts (Huck, Soltis & Coopersmith 1982; Labov et al. 1985; Manning et al. 1995). Among the 254 pup corpses that were not desiccated when we found them over the course of this study, 77.1% showed at least one such type of injury. There was no sign of injury on only 1.2% of these corpses. Information was missing for the remaining 21.7%. The three most common injuries observed in our population were the absence of a body part (38.6%), the presence of bites or open wounds (31.5%), and a hole in the skull (23.2%). Infanticide is so common in this population that it can sometimes be observed directly.

Genetic analyses: mother identity and number of sires

We extracted DNA from tissue samples taken from ears of pups found on the 13th day of age and from all adults as well as from pup corpses following the procedure detailed in Auclair et al (2014). A parentage analysis of these samples using 25 microsatellite loci (Auclair et al.

2014) provided the identity of the mother as well as the number of sires within litters to a 95% level of confidence using Cervus 3.0 (Kalinowski, Taper & Marshall 2007). Litters were categorized as genetically monandrous when they were sired by a single male and genetically polyandrous when they were sired by more than one male. Both paternity and maternity were successfully assigned to 146 litters produced by 106 females. An additional 143 litters disappeared entirely and were not accounted for in these analyses as no genetic material was available. There was no significant difference in the proportion of these that were solitary (N = 72) vs communal (N = 71) ($\chi^2 = 0.01$, df = 1, $p = 0.933$).

Communal vs solitary nests

Communal nests were defined as those containing litters from more than one mother, which was visually obvious only when pups in the nest differed in age. Therefore, we confirmed maternity using results of the genetic analyses which allowed us to identify 56 solitary litters and 90 communal litters.

Genetically vs socially polyandrous litters

The full parentage assignment of each litter provided the cumulated number of different sires within solitary and communal nests. Genetically monandrous litters raised in communal nests were categorized as genetically monandrous but socially polyandrous whenever they were associated with a litter sired by at least one different male.

Statistical analyses

All statistical tests were performed using R 3.0.2 (R Development Core Team 2013). Univariate and multivariate statistical analyses were used to examine pup survival. In the univariate analysis, pup survival was first categorized with respect to communal nesting and polyandry and then tested with independent Chi-square tests. In the multivariate analysis, pup survival was set as the response variable in a GLMM fitted with a binomial error distribution and corrected for over-dispersion. Mother identity was included as a random factor to control for non-independence of repeated measures from the same individuals. The fixed effects structure included communal nesting (measured as the number of different mothers within the nest), polyandry (measured as the number of different sires within the nest), pup age (at first census), population density, the two interactions involving communal nesting with polyandry and population density, and the interaction between polyandry and population density. The

significance of the fixed terms was given by Wald's tests. Following the recommendations of Nakagawa & Schielzeth (2013), we provide a full summary statistic of this model (Table 2).

Results

Polyandry and communal nesting

Although litters from communal nests were smaller than litters from solitary nests (communal litters: 3.31 ± 0.23 pups [mean ± SE] – range 1-8, solitary litters: 5.32 ± 0.27 pups – range 1-12; Student *t* test: t_{144} = -5.64, $p < 0.001$), they were sired by a similar number of males (communal litters: 1.37 ± 0.06 sires – range 1-4, solitary litters: 1.43 ± 0.08 sires – range 1-3; Wilcoxon test: $W = 2360.5$, $p = 0.439$).

The number of different sires within a nest showed a curvilinear increase with the number of litters pooled together ($R^2 = 0.36$; $F_{2,143} = 41.31$, $p < 0.001$; Fig. 1). Communal nests, which consisted of 2.85 ± 0.10 litters on average, summed more than twice as many sires as solitary nests (communal nests: 3.08 ± 0.18 sires – range 1-12, solitary nests: 1.43 ± 0.08 sires – range 1-3; Wilcoxon test: $W = 4293$, $p < 0.001$).

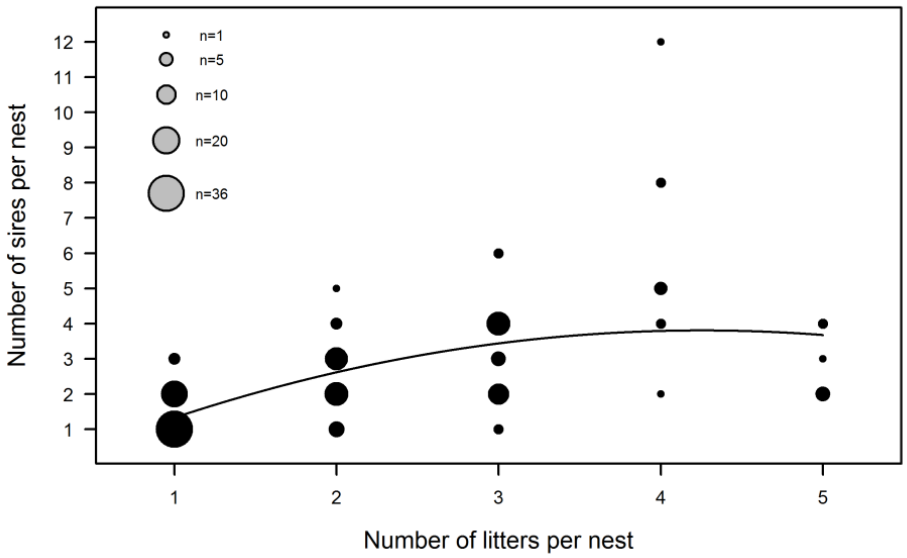

Figure 1. Positive correlation between the number of litters per nest and the number of different sires per nest. Figure shows observed data and regression line ($R^2 = 0.36$, $p < 0.001$).

Genetically polyandrous litters were as common in solitary nests as in communal nests ($\chi^2 = 1.00$, df =1, $p = 0.317$; Fig. 2a,b) whereas genetically monandrous litters were more often observed in communal nests than in solitary nests ($\chi^2 = 7.51$, df =1, $p = 0.006$; Fig. 2a,b). There was no significant difference between the number of genetically monandrous

and genetically polyandrous litters raised in solitary nests (χ^2 = 3.50, df =1, p = 0.061; Fig. 2a).

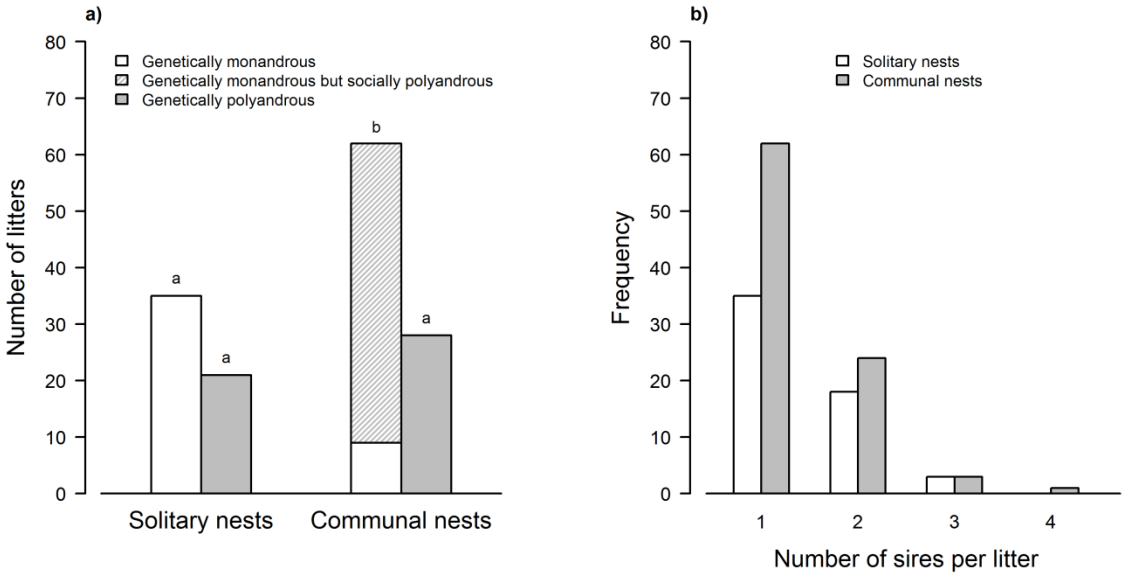

Figure 2. Distributions of (a) the litters according to communal nesting and polyandry (indices above columns (a,b) refer to significant differences between groups of data), and (b) the number of sires per litter within solitary and communal nests.

Univariate analysis of pup survival

Pup survival was significantly higher in communally raised litters than in solitarily raised litters (communal litters: 79.71 ± 4.23 % [mean ± SE_p (binomial standard error)], solitary litters: 56.71 ± 6.62 %; χ^2 = 3.88, df = 1, p = 0.049). Similarly to communal nesting, genetic polyandry (multiple paternity within litters) also significantly improved pup survival with polyandrous litters having a greater pup survival than monandrous litters (polyandrous litters: 81.39 ± 2.68 %, monandrous litters: 46.54 ± 5.75 %; χ^2 = 9.49, df = 1, p = 0.002).

Genetically polyandrous litters raised in solitary nests had a similar pup survival to those raised in communal nests (Table 1; Fig. 3). The same was observed between genetically monandrous litters raised in solitary nests or in communal nests. Genetically polyandrous litters, however, showed a higher pup survival than genetically monandrous litters, both within solitary nests and within communal nests. Socially polyandrous litters raised in communal nests showed a greater pup survival than that of genetically monandrous litters raised in communal nests as well as in solitary nests, and similar to that of genetically polyandrous litters regardless of whether they were raised in communal or in solitary nests.

Table 1. Summary table of the independent Chi-square tests used to compare offspring survival with respect to communal nesting and polyandry.

Comparison	χ^2	p
Solitary genetically monandrous vs Solitary genetically polyandrous	4.20	0.040
Solitary genetically monandrous vs Communal genetically monandrous	0.86	0.354
Solitary genetically monandrous vs Communal genetically polyandrous	9.70	0.002
Solitary genetically monandrous vs Communal genetically monandrous but socially polyandrous	10.43	0.001
Solitary genetically polyandrous vs Communal genetically monandrous	8.74	0.003
Solitary genetically polyandrous vs Communal genetically polyandrous	1.17	0.278
Solitary genetically polyandrous vs Communal genetically monandrous but socially polyandrous	1.45	0.229
Communal genetically monandrous vs Communal genetically polyandrous	16.02	< 0.001
Communal genetically monandrous vs Communal genetically monandrous but socially polyandrous	16.95	< 0.001
Communal genetically polyandrous vs Communal genetically monandrous but socially polyandrous	0.01	0.905

Multivariate analysis of pup survival

There was a significant interaction between the number of sires and the number of mothers (Table 2; Fig. 4). A greater number of sires within a nest significantly improved pup survival whereas the number of mothers alone had no significant effect (Table 2).

Although litters from communal nests were found when they were older than litters from solitary nests (communal litters: 2.30 ± 0.09 days [mean ± SE], solitary litters: 1.91 ± 0.11 days; t_{144} = 2.65, p = 0.009), the age at which the pups were found had no significant effect on pup survival (Table 2). Population density and its two interactions with polyandry and the number of mothers per nest had no significant effect on pup survival (Table 2).

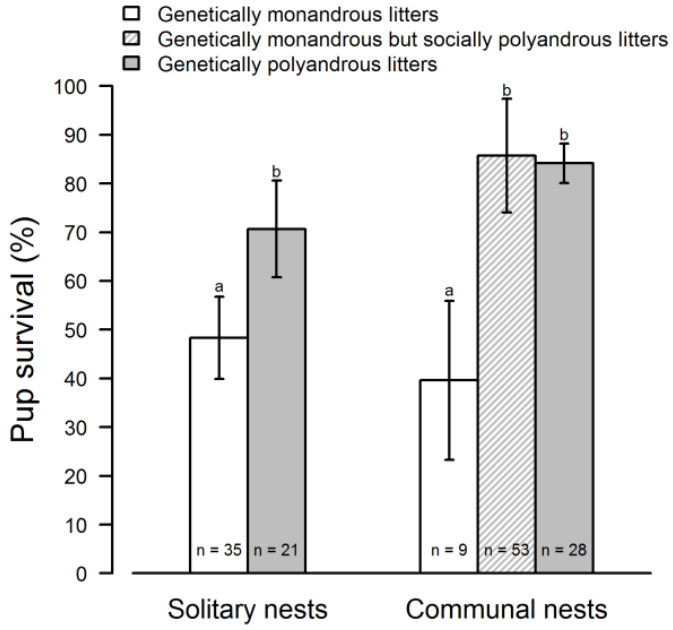

Figure 3. Influence of polyandry and communal nesting on pup survival (observed data ± SE_p). Indices above columns (a,b) refer to significant differences between groups of data.

Table 2. Full statistics of the mixed effect modeling of pup survival. The intercept of the full model represents a litter reared by 1 mother, sired by 1 male, found when 1 day old, at a population density of 44 adults.

	Null model	**Full model**	**Wald *Z***	***p***
Fixed effects	*b* [95% CI]	*b* [95% CI]		
Intercept	1.36 [0.91, 1.81]	-2.27 [-5.95, 1.41]	-1.21	0.228
Communal nesting (# mothers / nest)	—	0.42 [-1.95, 2.79]	0.34	0.730
Polyandry (# sires / nest)	—	2.64 [0.48, 4.80]	2.40	0.016
Pup age	—	0.46 [-0.04, 0.96]	1.80	0.071
Population density	—	-0.01 [-0.05, 0.03]	-0.48	0.630
Communal nesting (# mothers / nest) : Polyandry (# sires / nest)	—	-0.36 [-0.62, -0.10]	-2.71	0.007
Communal nesting (# mothers / nest) : Population density	—	0.01 [-0.01, 0.03]	0.59	0.555
Polyandry (# sires / nest) : Population density	—	-0.01 [-0.03, 0.01]	-1.08	0.278
Random effects	VC	VC		
Mother identity	1.530	1.468		
Observations (correction for over-dispersion)	2.830	2.219		
Residuals	—	—		
Fixed effects	—	1.685		
$R^2_{\text{GLMM (m)}}$	—	19.45%		
$R^2_{\text{GLMM (c)}}$	—	62.02%		

CI: Confidence Interval; —: not applicable/available; VC: Variance Components; $R^2_{\text{GLMM(m)}}$: marginal R^2 for GLMM (i.e variance explained by fixed factors); $R^2_{\text{GLMM(c)}}$: conditional R^2 for GLMM (i.e variance explained by fixed and random factors).

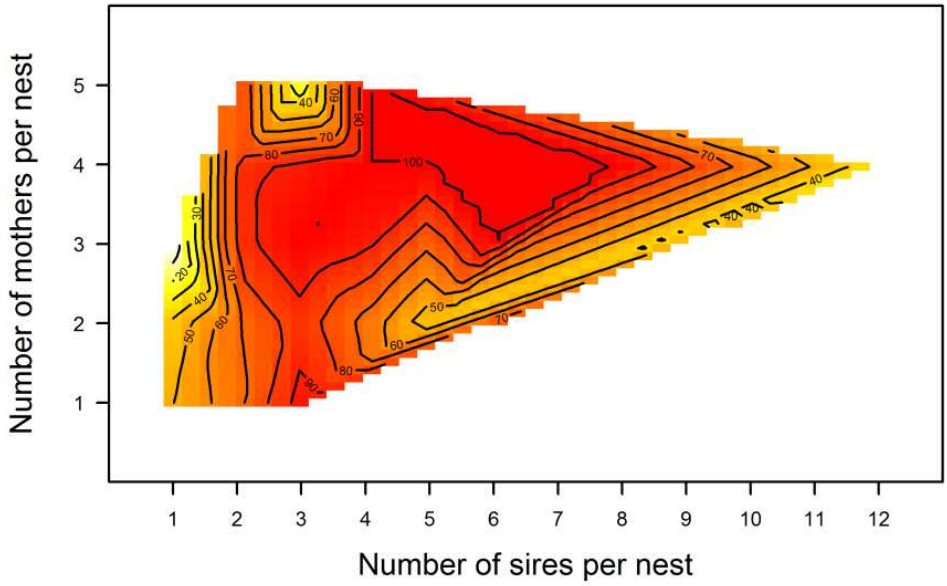

Figure 4. 3-D representation of the interaction between the number of sires and the number of mothers within a nest on pup survival (isoclines represent pup survival in %; colour increases gradually from yellow to red with increasing pup survival).

Discussion

Communal nesting and multiple paternity of litters both improved offspring survival in wild house mice. However, we showed that nests containing offspring sired by multiple males survived better than nests containing offspring sired by a single male, both in solitary and communal nests. Mating with multiple males allows polyandrous females to confuse the paternity of their litters hence preventing males from committing infanticide as they could kill their own offspring (Klemme & Ylönen 2010; Perrigo, Bryant & vom Saal 1990; van Schaik et al. 2000; Wolff & MacDonald 2004). We therefore suggest that paternity confusion is the mechanism responsible for the higher offspring survival associated with communal nesting. If males are unable to recognise their young, but refrain from attacking offspring in a nest attended by a female with which they previously mated, then nests in which there are more potential fathers are better protected. A female that has not mated polyandrously would benefit from socially mediated polyandry, by associating her offspring with offspring of other females that mated with different males to herself, in a communal nest.

Our hypothesis would be falsified if: 1) offspring mortality does not reflect infanticide, 2) males could discriminate their offspring from others within a communal nest, 3) polyandry does not result in multiple paternity, 4) females within a communal nest had the same mating

partners, 5) communal nesting is not the result of an active choice. Each of these points, however, can be addressed.

1) As the population studied here was not exposed to nest predation, postnatal offspring mortality could only be explained by postpartum cannibalism by the mother, abandonment, disease or infanticide. Both postpartum cannibalism and abandonment are expected to occur very soon after birth so that mothers avoid wasting energy in costly maternal care such as lactation (Hammond & Diamond 1992). Because we first found litters when they were on average two days old, postpartum cannibalism and abandonment are not very likely to explain offspring mortality in our population. Although restricted food availability has been shown to promote cannibalism of older pups by lactating females (König 1989b), this should not occur in our population as food was provided *ad libitum*. Moreover, nearly all pups we found looked healthy (were of normal appearance and did not show deformities). Infanticide, on the other hand, is very common in rodents and other taxa (Hrdy 1979). For instance, a field study showed that 51% of the litters suffered infanticide in black-tailed prairie dogs *Cynomys ludovicianus* (Hoogland 1985). Since most of the dead pup corpses we collected displayed injuries typical of infanticide and since infanticide was also occasionally directly observed, we think that most of the offspring mortality observed in our population resulted from infanticide. Previous studies suggested that the presence of conspecifics is a better predictor of juvenile mortality than the presence of predators which is considered as insignificant (Berry 1970; Berry & Bronson 1992; Brown 1953; Southwick 1955). Consequently, the substantial effect that predation could have on offspring survival is not very likely to mask the benefits of polyandry.

2) There is little evidence that males can recognize own offspring in altricial birds and mammals (Blaustein, Bekoff & Daniels 1987; Kempenaers & Sheldon 1996; Mateo 2003). In the house mouse, the most convincing evidence of male kin recognition showed that males use prior matings with a female, more particularly those that included ejaculation, to assess their affiliation with her offspring (Huck et al. 1982; McCarthy & vom Saal 1986; Perrigo, Bryant & vom Saal 1989; Perrigo et al. 1990). Female house mice also have very limited if any ability to recognize own offspring (Hager & Johnstone 2005; König 1989a, b).

3) The category of "singly sired" litters will include females that mated with only one male as well as those that mated multiply, especially when litter sizes are small (Neff, Pitcher & Repka 2002). The number of different sires within litters is likely to underestimate the actual frequency of multiple mating as there is a high post-copulatory competitive skew between males in house mice (Dean et al. 2006; Levine 1967). In our study we assume that

females with multiply sired litters had more mating partners than those with singly-sired litters.

4) We found that only 10% of the litters found in communal nests were pooled with litters sired by the same male. Thus, nearly all communal nests could benefit from paternity confusion.

5) Communal nests in the study population are the result of female choice. Females choose among available nesting partners (Weidt et al. 2014). Experimental evidence shows that when females that prefer each other initiate a communal nest, reproductive success is higher than in nests of females that had no preference for each other (Weidt, Hofmann & König 2008). Here, we found a higher proportion of females whose litters were singly sired in communal nests compared to solitary nests, raising the possibility that these females may actively try to socially acquire the benefits of polyandry.

Taken together, the evidence is convincing that our new hypothesis can be applied to communal nesting in wild female house mice. Firstly, we demonstrated that females benefit from polyandry. This may explain why multiple paternity was similar among females raising their offspring in solitary or communal nests. Moreover, the prevalence of multiple paternity renders the wide-spread assumption of a polygynous mating system in house mice questionable (Latham & Mason 2004). Secondly, polyandry can explain the offspring survival advantage associated with communal nesting. Communal nesting can benefit monandrous females by reducing the risk from male infanticide through socially mediated polyandry when litters are pooled with others sired by different males. Furthermore, females who have the option to communally nest could potentially avoid costs of polyandry (Clutton-Brock & Parker 1995; Parker & Birkhead 2013; Stockley 1998) and mate with their preferred male.

It has been proposed that more females sharing a communal nest could correlate with an increased nest defence (see Manning et al. 1995). For this hypothesis to hold true, all litters from communal nests should show a better offspring survival than those from solitary nests. Our data, however, do not support this hypothesis as illustrated in Figures 3 and 4. Furthermore, we found a significant interaction between the number of females and the number of sires within a nest, indicating that the offspring survival benefits of polyandry are modified by the number of females at the nest, pointing to a complex role of social structure in offspring survival. Previous studies have demonstrated the limited influence of maternal aggression in preventing infanticide perpetrated by male house mice hence suggesting that paternity confusion may be more efficient against male infanticide (Palanza, Parmigiani & Vom Saal 1995). As an alternative to an increasing number of females who could defend a

nest, offspring survival may be improved through a better coordination between these females. Relatedness does not only help stabilizing the relationship between cooperative partners, but it can also improve the outcome of their interaction (Holmes & Sherman 1982). A recent study, however, showed that relatedness between communally nesting females had no effect on patterns of nest attendance or the time their litters are left alone (Auclair et al. 2014).

Previous hypotheses for communal nesting include the non-adaptive hypothesis of misdirected maternal care as a by-product of social living (Hayes 2000; Pusey & Packer 1994; but see Weidt et al. 2014), and the hypotheses that communal nesting is adaptive *via* offspring thermoregulation benefits (Hayes & Solomon 2006), improved offspring milk intake and growth rate (Heiderstadt & Blizard 2011; Mennella et al. 1990; Sayler & Salmon 1969), better offspring immunity (Boulinier & Staszewski 2008; Roulin & Heeb 1999) and higher female reproductive success (König 1994). We provide here a new adaptive hypothesis for the evolution of communal nesting where females who produced litters sired by a single male can improve the survival of their offspring by pooling their litters with others sired by different males, which we call socially mediated polyandry. This socially mediated polyandry was as efficient as genetic polyandry in improving offspring survival. Our new hypothesis may not only apply to the other species known for providing communal care to their offspring which represents 15% of all mammalian species in more than seven orders (Eisenberg 1981). Any polytocous vertebrate producing litters of more than one offspring, in which infanticide is a behavioural strategy, and where the caring parent exhibits social behaviours could also be a good candidate.

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Maternal investment strategy in wild house mice: no evidence for a benefit of weaning heavier offspring

To be submitted

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Maternal investment strategy in wild house mice:
no evidence for a benefit of weaning heavier offspring

Yannick Auclair, Barbara König & Anna K. Lindholm

Institute of Evolutionary Biology and Environmental Studies, University of Zurich,
Winterthurerstrasse 190, CH-8057 Zurich, Switzerland

Abstract

How much individuals should invest into parental care to maximize the fitness of their offspring is a particularly acute question in mammals, in which maternal investment via lactation predicts offspring growth rate to weaning. As body mass is often associated with fitness consequences, females have the potential to influence their offspring lifetime fitness through their level of investment. Using lifetime fitness data of 384 non-dispersing mice from a free-living wild population we assessed the extent to which mothers influenced the body mass of their offspring at weaning and once adult. Then, we looked whether body mass at weaning influenced individuals' reproductive success and longevity while controlling for sex and population density. Results showed that mothers contributed to 49% and 14% of the variance observed in offspring body mass at weaning and once adult, respectively. Body mass at weaning had a weak influence on adult body mass and had no influence on the age at first reproduction or the number of offspring weaned over a lifetime. Longevity, however, was shorter for the heaviest offspring which may result from their higher likelihood to become dominant and be involved in agonistic interactions after weaning. Moreover, males lived shorter than females which may result from sex differences in social behaviour. An increase in population density delayed the first reproduction most likely because of an increased reproductive competition. This study shows no evidence for a benefit of a higher postpartum maternal investment and suggests that females may rather invest in offspring quantity than quality.

Keywords: Body mass – Longevity – Maternal effects – Population density – Primiparity – Reproductive success – Sexual dimorphism

Introduction

Early life is a critical period for newborns as any stress can have long-term irreversible consequences on their morphology (Lummaa & Clutton-Brock 2002; Tschirren et al. 2009), physiology (Mirescu, Peters & Gould 2004; Sebaai et al. 2004), immunology (Edwards & Cooper 2005; Prager et al. 2010) or behaviour (Laviola & Terranova 1998; Levitsky & Barnes 1972; Lovic, Gonzalez & Fleming 2001). The future life history strategies followed by individuals may therefore be shaped by the conditions experienced during their early life (Lindström 1999; Metcalfe & Monaghan 2001). Parents, however, only have a finite quantity of energy to invest into reproduction as suggested by the negative relationship between brood size and offspring quality observed in a wide range of taxa (Charnov & Ernest 2006; Lack 1947; Roff 2002). How much energy parents should allocate to a given reproductive event in order to maximize the fitness of their offspring remains a long-standing question in life history theory (Gittleman & Thompson 1988; Lloyd 1987; Stearns 1992).

The importance of parental investment can be appreciated through maternal effects (Maestripieri & Mateo 2009b; Mousseau & Fox 1998; Reinhold 2002). Maternal effects are defined as the effects of a mother's phenotype on the phenotype of her offspring (Wolf & Wade 2009). This maternal source of variance in offspring phenotype can be partitioned into prenatal maternal effects like egg size, and postnatal maternal effects like maternal behaviour. In species where newborns have a prolonged period of maternal dependence until weaning, the contribution of postnatal maternal effects on offspring body size can outweigh that of prenatal maternal effects (Reinhold 2002; Steiger 2013). Postnatal maternal investment is not only influenced by the number of offspring but the sex ratio of a brood or a litter may also affect the overall maternal investment whenever one sex is more costly to rear (Gomendio et al. 1990).

Mammals give birth to altricial young who cannot feed or thermoregulate at birth. In most species, females provide all the parental care with lactation being the most important parental investment component (Gittleman 1985). Previous studies have shown that lactation can explain up to 65% of the variation observed in body mass at weaning in the house mouse *Mus domesticus* (Atchley & Zhu 1997; Cox, Legates & Clark Cockerham 1959; El Oksh, Sutherland & Williams 1967). Offspring body mass at weaning correlates with maternal investment (Don Bowen et al. 2001; Falconer 1947; Mateo 2009; McDowell, Gates & McDowell 1930). Weaning therefore represents the best time point to assess cumulative maternal energy allocation (pre- and postnatal). Body mass at weaning represents a good alternative to direct metabolic measurements of parental investment that are often too

complicated or invasive to be used on wild populations (König, Riester & Markl 1988; Sadowska, Gebczynski & Konarzewski 2013).

There are many examples reporting the benefits of being relatively heavier from small mammals to large herbivores. Although population density should not be ignored when looking at life history traits (Clutton-Brock 1988; Gaillard et al. 1997; Gilbert & Krebs 1991; Saitoh 1981), heavier individuals usually have a higher probability of settlement in their population (Wauters, Bijnens & Dhondt 1993), can achieve higher dominance ranks (e.g Klemme, Ylönen & Eccard 2007; Krackow 1993), reproduce earlier and/or produce more offspring (e.g Anderson & Fedak 1985; Dobson & Michener 1995; Festa-Bianchet, Jorgenson & Réale 2000; Fuchs 1982) or survive better (e.g Millar & Hickling 1990; Murie & Boag 1984; Wauters & Dhondt 1989). Moreover, body mass is considered a reliable proxy for the quality or health of an individual (Oli & Dobson 2003; Peters 1986). The influence of size on performance is not only observed at adulthood but can also be detected at earlier stage of life (Dias & Marshall 2010). The positive relationship between offspring and adult body mass (Birgersson & Ekvall 1997; Festa-Bianchet et al. 2000) and the increased offspring quality at weaning observed whenever offspring received extended maternal care (Dahle & Swenson 2003) suggest that a higher maternal investment could improve offspring lifetime fitness.

The present study addressed this question using long-term data from an intensively monitored wild population of house mice. After assessing the influence of mothers on the body mass of their offspring at weaning while controlling for litter size and the sex of the offspring, we assessed the mothers' influence and the independent effect of body mass at weaning on adult body mass. Then, we tested whether offspring body mass at weaning could predict longevity and lifetime reproductive success, measured as the age at first reproduction and as the number of offspring weaned, while accounting for sex differences and population density.

Material and methods

Study population

Data were collected from a free-living house mouse population in a $70m^2$ building in Illnau, Switzerland. Although mice can easily exit the building through numerous gaps, none of the mammalian and avian predators that occur outside can enter. The high permeability of the building towards mice does not allow the collection of emigration data. Water and food, a 50/50 mixture of oats and hamster food (Landi AG, Switzerland), were provided *ad libitum* to match conditions under which natural house mouse populations are typically observed in

Western Europe (Berry 1970). The entire population inside the building was captured on average every seven weeks to estimate adult population density and to examine animals.

Reproductive activity

Reproduction occurred in 40 artificial nest boxes. We searched for new litters approximately every 10 days between January 2007 and December 2009. Each new litter was given an identification number, the litter size was recorded, and the pups were sexed according to their anogenital distance and genital morphology (Hotchkiss & Vandenbergh 2005), and aged according to morphological development. Skin pigmentation, development of the ears, growth of the fur, teeth eruption, and eye development give reliable cues about the age of the pups (day of birth was considered as day 1).

Body mass measurements

Pups were weighed to the nearest 0.1g when they were 13 days old (±1 day). This age is the last day before weaning when they can be reliably captured as they are still blind, largely immobile and fully dependent on milk (König 1993). In captures of the entire population, each individual was weighed to the nearest 0.1g and those weighing at least 16g were considered adults (Pelikán 1981). Because the population is captured every seven weeks, individuals differ in the age at which they were first captured as adults.

Genotyping and parentage analysis

An ear tissue sample was collected from every pup and adult that was weighed, and on all corpses found. Following the same procedure as in Auclair et al. (2014), DNA was amplified using 25 microsatellite loci and a parentage analysis allowed assignment of the mother and the father of each individual to a 95% level of confidence using Cervus 3.0 (Marshall et al. 1998). Only fully assigned offspring and corpses that gave good quality DNA were kept in the data.

Fitness estimates

Individual reproductive success was assessed using genetic parentage analyses and separately defined as both age at first reproduction, and total number of weaned offspring (defined as surviving to 13 days of age) throughout life. The total of offspring weaned was monitored for a total of 384 pups (167 females and 217 males) born between January 2007 and December 2009 from 178 litters produced by 120 mothers. Among these 384 individuals, 219 (100

females and 119 males) reproduced so their age at first reproduction was available (produced a total of 2631 pups). The collection of corpses also allowed us to calculate longevity for 147 (56 females and 91 males) of these 384 individuals. The last corpse was collected on March 26th 2012 and the latest detection of a living focal individual in the building was on February 21st 2012.

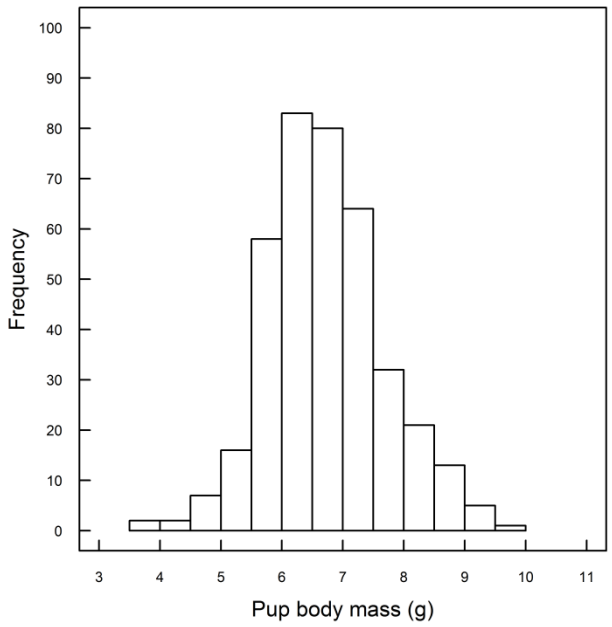

Figure 1. Distribution of pup body mass.

Statistical analyses

Statistical tests were carried out using R 3.0.2 (R Development Core Team 2013). The influence of mother identity, litter size, sex, and sex ratio on pup body mass was assessed using a linear mixed-effects model (Bates, Maechler & Bolker 2012). Mother identity was defined as a random factor while sex ratio, litter size, pup sex and the interactions between litter size and pup sex, and between litter size, sex, and sex ratio were defined as fixed factors. The quadratic term of litter size was added to the fixed factors as it significantly improved the fit of the model (quadratic vs only linear: Δ_{AIC} = -6, R^2_{LMM} (m) = 3.99% vs 2.19%, R^2_{LMM} (c) = 51.01% vs 48.64%; LRT: χ^2 = 10.43, p = 0.005). The influence of mother identity on the adult body mass of the offspring was assessed with a separate linear mixed-effects model with mother identity defined as a random factor and pup body mass, sex, and their interaction defined as fixed factors. The contribution of mother identity was estimated as the proportion of the total variance explained by the random factor "mother identity" and tested by a likelihood ratio test comparing this model to a generalized least square model having the same fixed factors structure but no random factor (Zuur et al. 2009). The significance of the

fixed effects was determined with F-tests. Additionally, we provide a full summary statistic of the mixed-effects modelling following Nakagawa & Schielzeth (2013) (Table 1).

The influence of pup body mass on longevity and age at first reproduction was analysed with two independent linear models accounting for pup body mass, sex, population density, and their second degree interactions. The number of offspring weaned was analysed with a zero inflated model with the same fixed effects structure but fitted for a negative binomial distribution of the errors (Zeileis, Kleiber & Jackman 2008). Significance of the fixed effects was tested using F-tests in the two linear models whereas likelihood ratio tests were used in the zero inflated model.

Results

Influence of mother identity, sex, sex ratio, and litter size on pup body mass

Differences between mothers accounted for 49.0% of the total variance observed in pup body mass (χ^2 = 89.13, df = 1, p < 0.001; Table 1; Figure 1). Pup body mass was not significantly influenced by sex ($F_{1,256}$ = 1.66, p = 0.198), sex ratio ($F_{1,256}$ = 0.11, p = 0.744) or the third degree interaction between litter size, sex and sex ratio ($F_{2,256}$ = 1.55, p = 0.213). However, litter size ($F_{2,256}$ = 3.24, p = 0.041) and its interaction with sex ($F_{2,256}$ = 5.11, p = 0.007) were significant. Although pup body mass did not covary with litter size in females, male pup body mass was higher in litters of intermediate size than in small or large litters (Figure 2).

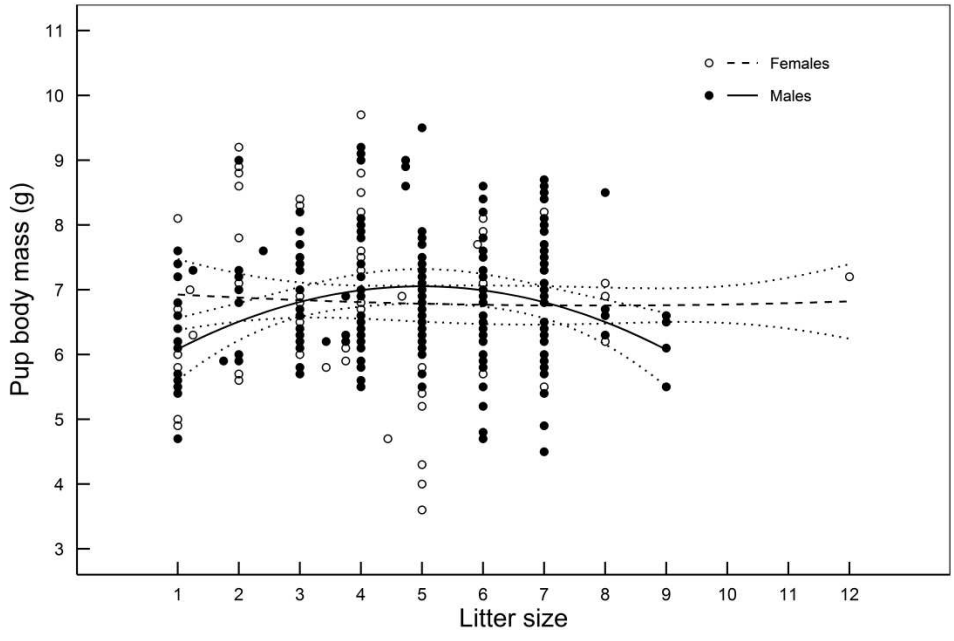

Figure 2. Influence of litter size on pup body mass. Figure shows model predictions ± 95% CI.

Influences of mother identity, pup body mass, and sex on adult body mass

As adult body mass increased with age, the measure of body mass had to be corrected for the age when individuals have been weighed. A negative exponential function has therefore been fitted to the data and the residuals have been used as a proxy for adult body mass in further analyses (R^2 = 0.32; y= 35.94 - 17.57*$e^{(0.002*x)}$; Figure 3).

Mother identity accounted for 13.8% of the total variance observed in the adult body mass of her offspring (χ^2 = 6.52, df = 1, p = 0.011; Table 1). Once adult, males were significantly heavier than females ($F_{1,261}$ = 116.25, p < 0.001; Males: 1.14 ± 0.16 residual body mass [mean ± SE], Females: -1.48 ± 0.19 residual body mass). Furthermore, the significant interaction between pup body mass and sex indicated a positive relationship between pup and adult body mass in males whereas there was no relationship between these two variables in females ($F_{1,261}$ = 4.24, p = 0.040; Figure 4). Pup body mass alone ($F_{1,261}$ = 3.59, p = 0.059) had no significant effect on adult body mass.

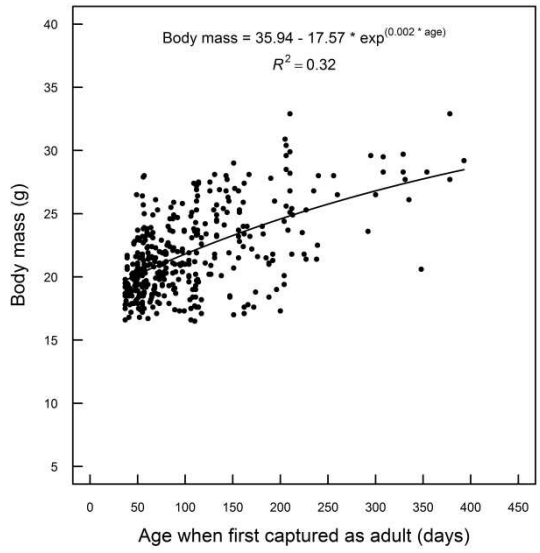

Figure 3. Non-linear relationship between body mass and the age when first captured as an adult. Residuals have been used as "adult body mass" for further analyses.

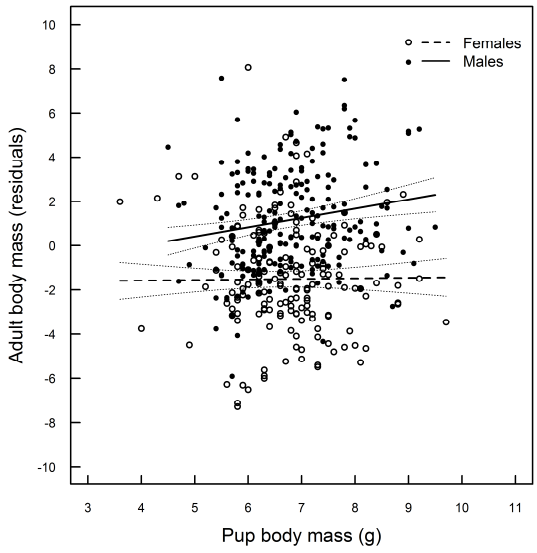

Figure 4. Influence of pup body mass on adult body mass. Figure shows model predictions ± 95% CI.

Lifetime fitness consequences of pup body mass

The age at first reproduction was not significantly influenced by pup body mass but adult population density at birth, however, significantly delayed the first reproduction (Table 2). More particularly, the first reproduction occurred later when population density was higher (Figure 5). Neither sex nor any of the second degree interactions between pup body mass, sex, and population density had a significant effect (Table 2).

Table 1. Summary of the mixed-effects modelling of a) pup and b) adult body mass. CI: Confidence Interval; —: not applicable/available; VC: Variance Components; PCV: Proportion Change in Variance; $R^2_{LMM(m)}$: marginal R^2 for LMM (i.e variance explained by fixed factors); $R^2_{LMM(c)}$: conditional R^2 for LMM (i.e variance explained by fixed and random factors); AIC: Akaike Information Criterion.

a)

	Pup body mass	
	Null model	Full model
Fixed effects	*b* [95% CI]	*b* [95% CI]
Intercept	6.77 [6.62, 6.91]	6.67 [6.46, 6.88]
Litter size	—	-1.53 [-4.92, 1.86]
Litter size^2	—	-0.16 [-2.68, 2.36]
Sex (female vs male)	—	0.07 [-0.17, 0.31]
Sex ratio	—	0.10 [-0.24, 0.44]
Litter size : Sex	—	-8.56 [-18.76, 1.64]
Litter size^2 : Sex	—	-4.18 [-7.93, -0.43]
Sex (female) : Litter size : Sex ratio	—	-0.04 [-0.34, 0.26]
Sex (male) : Litter size : Sex ratio	—	0.36 [0.07, 0.65]
Random effects	VC	VC
Mother identity	0.415	0.465
Residuals	0.535	0.486
Fixed factors	—	0.040
$PCV_{[mother\ identity]}$	—	10.75%
$PCV_{[residuals]}$	—	-10.08%
$R^2_{LMM\ (m)}$	—	3.99%
$R^2_{LMM\ (c)}$	—	51.01%
$AIC_{(maximum\ likelihood)}$	989	984

b)

	Adult body mass	
	Null model	Full model
Fixed effects	*b* [95% CI]	*b* [95% CI]
Intercept	-0.06 [-0.39, 0.27]	-1.51 [-1.12, -1.90]
Pup body mass	—	-0.06 [-0.44, 0.32]
Sex (female vs male)	—	2.60 [2.13, 3.07]
Pup body mass : Sex	—	0.53 [0.02, 1.03]
Random effects	VC	VC
Mother identity	0.868	0.753
Residuals	6.581	4.932
Fixed factors	—	1.774
$PCV_{[mother\ identity]}$	—	-15.27%
$PCV_{[residuals]}$	—	-33.43%
$R^2_{LMM\ (m)}$	—	23.57%
$R^2_{LMM\ (c)}$	—	34.10%
$AIC_{(maximum\ likelihood)}$	1861	1758

Table 2. Influence of pup body mass, sex, population density, and their second degree interactions on individuals' lifetime fitness as measured by the age at first reproduction, number of offspring weaned, and longevity.

Fitness estimates	Explanatory variables	*F-test / Likelihood ratio test*	*p*
Age at first reproduction N = 219	Pup body mass	$F_{1,218} = 0.91$	0.342
	Sex	$F_{1,218} = 0.98$	0.322
	Population density	$\mathbf{F_{1,218} = 51.87}$	**< 0.001**
	Pup body mass : Sex	$F_{1,218} = 0.04$	0.849
	Pup body mass : Population density	$F_{1,218} = 3.25$	0.073
	Sex : Population density	$F_{1,218} = 1.37$	0.242
Lifetime reproductive success (#offspring weaned) N = 384	Pup body mass	$\chi^2 = 0.13$	0.715
	Sex	$\chi^2 = 0.13$	0.714
	Population density	$\chi^2 = 0.82$	0.366
	Pup body mass : Sex	$\chi^2 = 0.01$	0.917
	Pup body mass : Population density	$\chi^2 = 2.90$	0.088
	Sex : Population density	$\chi^2 = 0.04$	0.830
Longevity N = 147	**Pup body mass**	$\mathbf{F_{1,146} = 4.32}$	**0.039**
	Sex	$\mathbf{F_{1,146} = 46.75}$	**< 0.001**
	Population density	$F_{1,146} = 1.04$	0.309
	Pup body mass : Sex	$F_{1,146} = 1.08$	0.300
	Pup body mass : Population density	$F_{1,146} = 1.07$	0.303
	Sex : Population density	$F_{1,146} = 2.82$	0.095

Individual lifetime reproductive success, as measured by the number of offspring weaned over a lifetime, was not significantly influenced by pup body mass, sex, population density or their second degree interactions (Table 2).

Longevity significantly differed in regards to the sex of the individuals (Table 2). Females lived longer than males (Males: 294 ± 13 days, Females: 459 ± 24 days; Figure 6). Moreover, pup body mass had a significant negative influence on longevity (Table 2; Figure 6). Population density alone, its interactions with pup body mass and sex, and the interaction between pup body mass and sex had no significant effect on longevity (Table 2). There was no bias in the sex ratio of the 237 individuals for which we found no dead bodies and assume they died outside of the building (111 females vs 126 males; $\chi^2 = 0.95$, df = 1, $p = 0.330$).

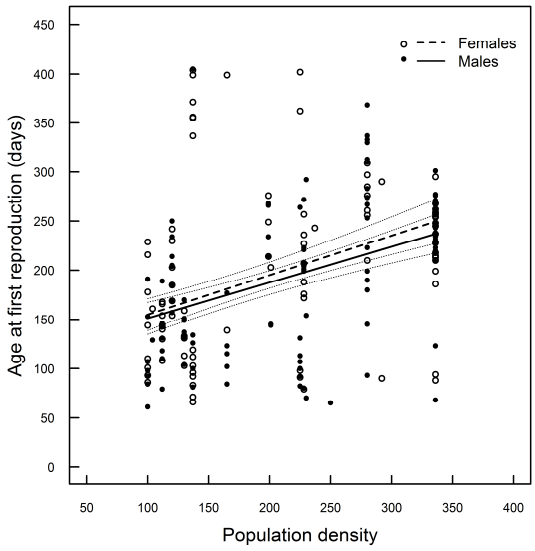

Figure 5. Influence of population density on the age at first reproduction. Figure shows model predictions ± 95% CI.

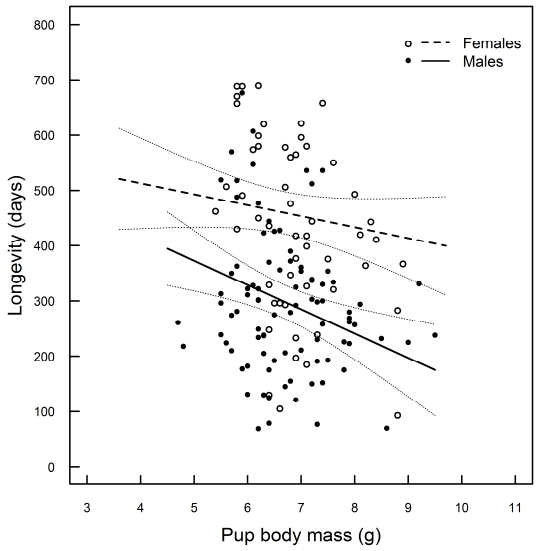

Figure 6. Influence of pup body mass on longevity. Figure shows model predictions ± 95% CI.

Discussion

The aim of this study was to investigate the extent to which mothers can influence the body size of their offspring and to examine the lifetime fitness consequences of variation in offspring body size. Differences between mothers were responsible for about 49% of the total variance in offspring body mass, a contribution that decreased to 14% of the adult body mass of the same offspring. These estimates do not distinguish between causal factors underlying variation between females (maternal effects, genetic effects, other environmental effects). In house mice, however, carefully controlled cross-fostering experiments have shown that

maternal effects exhibit by far the strongest effect on variation in offspring body mass before weaning (Wolf et al. 2011). The substantial amount of maternal effects observed on offspring body mass is relatively high in mammals due to the long period of offspring maternal dependence for nutrition (see also Maestripieri & Mateo 2009a; Reinhold 2002). However, conversely to additive or environmental effects, maternal effects cannot generate further phenotypic variation after maternal care ceases. This explains why the relative contribution of maternal identity on the overall phenotypic variation of a trait decreases through ontogeny while additive effects usually increase (Lindholm, Hunt & Brooks 2006; Wilson & Réale 2006; Wolf et al. 2011).

The large influence of the mothers on the development of their offspring to weaning suggests that they may have the possibility to strongly affect offspring lifetime fitness. Our results, however, did not show any effect of offspring body mass on the age at first reproduction or the number of offspring weaned. We expected that a heavier weaning weight would allow an earlier onset of reproduction hence leading to a higher reproductive success (Roff 2002). In many taxa, larger individuals have higher reproductive success (Dias & Marshall 2010). In mammals, bigger males typically have higher chances to acquire a breeding territory, become dominant and reproduce (Anderson & Fedak 1985; Bouteiller-Reuter & Perrin 2005; Clutton-Brock et al. 1979; Oakeshott 1974). Such advantages towards big individuals are not limited to males as intra-sexual competition also occurs within females (Stockley & Bro-Jørgensen 2011). Female competition may occur to control territories housing the best nest sites or to control the access to food (Bujalska 1973; Ostfeld 1985; Reimer & Petras 1967; Wolff 1993). Similarly to males, reproductive success can be skewed toward dominant females (Clutton-Brock, Albon & Guinness 1984; Rusu & Krackow 2004). Laboratory studies of mice have shown that larger females produce larger litters and have shorter inter-birth intervals during their first two reproductive events (Fuchs 1982). The strong intra-sexual competition acting in both sexes may explain the shorter survival of the heaviest offspring independently from genetic particularities affecting growth rate and then longevity (Miller et al. 2002). Large offspring may experience more frequent agonistic interactions that may compromise their survival compared to their smaller counterparts. They may be perceived as a threat and attacked by dominant individuals and their higher likelihood to become dominant increases their risk to be injured or killed while being repeatedly challenged by subordinates (Oakeshott 1974). Social competition may, however, be different between sexes (Stockley, Bottell & Hurst 2013). For instance, the evolution of physiological suppression in females may help in decreasing the rate of aggressions within this sex and may

contribute to their survival advantage over males (Clutton-Brock et al. 1979; Clutton-Brock & Isvaran 2007; Clutton-Brock 2009).

Apart from the effect of the mother, the social environment was important both in offspring body mass and in offspring fitness components. In male offspring, body mass showed a curvilinear relationship with litter size, in line with theoretical predictions (Charnov & Ernest 2006). In females, however, litter size had no effect on body mass. This sex difference could be due to sex-differential allocation but this is unlikely in house mice because the immobile arched posture of nursing females limits their control of access to the nipples (König 1989a). Furthermore, sex ratio within the litter did not influence offspring body mass. Male offspring may be more costly to wean than female offspring or may have higher energy requirements and therefore be more sensitive to poor maternal investment (Clutton-Brock, Albon & Guinness 1985; Lindström 1999; Teather & Weatherhead 1988). Male and female pups may differ in their behaviour or metabolism (Garel et al. 2009), as seen in spotted hyenas *Crocuta crocuta* (Golla, Hofer & East 1999) and sea lions *Zalophus californianus* (Ono & Boness 1996). An inter-sibling competition favouring the access to milk in one sex or a sex differential digesting efficiency have, however, never been reported in house mice. Population density was also an important social factor as it influenced the age at which individuals started to reproduce. Similarly to what has been reported in other mammals, the delay in the onset of reproduction is likely to be due to an increase in the reproductive competition or a reduction in the number of available nesting sites (Gilbert & Krebs 1991; Jorgenson et al. 1993; Saitoh 1981) (Komers, Pélabon & Stenström 1997). Individuals who are poor competitors are thus more likely to deliberately defer their reproduction and queue to acquire breeding or social positions (Kokko & Johnstone 1999; van de Pol et al. 2007).

The distribution of offspring body mass in our population showed a surprising dispersion given that milk production is energetically expensive, increasing females' basal metabolic rate by up to 7.2 times (Hammond & Diamond 1992; König et al. 1988), and that we found no evidence for fitness consequences of body size. Reducing female investment in milk, leading to smaller offspring size, could benefit females. Lowering their current maternal investment would allow females to raise their investment in the next reproduction, to shorten inter-birth intervals, or favour longevity (Metcalfe & Monaghan 2013; Simpson et al. 1981; Trivers 1972). More puzzling is understanding why females would seemingly over-invest in maternal care and produce heavy offspring which have no fitness advantage over lighter offspring. Parental care decisions involve trade-offs on the costs of reproduction such as the

costs of current reproduction on future reproduction or survival (Koivula et al. 2003), but also between offspring number and quality (Kaufman & Kaufman 1987). Individuals are therefore expected to tune their parental investment in regards to factors such as brood size, past investment, the age of the caring parent, its health, the timing of the reproduction (beginning or end of the reproductive season or lifespan) or food availability (Coleman, Gross & Sargent 1985; Klug, Alonzo & Bonsall 2012; Myers & Master 1983). The ready access to food in the study population might have substantially lowered the costs of maternal investment. However, our study reflects natural conditions for house mice in Western Europe, as house mice live commensally with humans, and populations usually grow wherever food is easily accessible and available in good quantity (Berry 1970; Latham & Mason 2004; Pocock, Searle & White 2004). Milk yield is a direct function of food intake (Mann et al. 1983; Myrcha, Ryszkowski & Walkowa 1969) and females may be willing to undertake high costs of lactation (Hammond & Diamond 1992; König et al. 1988; Myrcha et al. 1969) under such circumstances of easy access to food. Furthermore, reproduction is highly skewed in house mice and the majority of females who access reproduction might reproduce only once (Rusu & Krackow 2004). It is thus possible that these females invest more than what would be optimal. Populations of house mice in which females are constrained in the amount of energy they can dedicate to offspring care, because of food scarcity or monopolization by a small number of individuals, are predicted to show different results to the ones presented here. For instance, König (1989b) showed that offspring body mass at weaning decreased when mothers were kept under a restricted food diet. Conversely, females can increase the time course of weaning, hence their investment, whenever food resources are more important than expected (Berger 1979; Lee 1984).

Communal nesting, when females pool their litters together in a single nest and share all maternal duties including nursing, could provide another explanation to a maternal over-investment (Hayes 2000; König 2006). This cooperative behaviour, observed in a third of nests (Weidt, Lindholm & König 2014), can allow communally nesting females to improve milk yield (quantity or quality) through their reduced nest attendance which allows more time for foraging (Auclair et al. 2014; Kretzmann et al. 1991). Furthermore, offspring could benefit from more regular meals (Auclair et al. 2014) hence favouring higher growth rates independently of changes in female milk yield.

As this study only looked at long-term fitness consequences of maternal investment, it is possible that females' extra-investment may have short-term fitness consequences for the offspring such as a better survival between weaning and sexual maturity. Moreover, the social

complexity of house mice societies suggests that the effect of social competence on reproductive success may outweigh those of body size at weaning (König & Lindholm 2012; Taborsky & Oliveira 2012).

In response to the absence of fitness benefits associated with offspring size at weaning the dams may limit their investment to a level that only ensures offspring survival after weaning (König & Markl 1987). As offspring mass did not have a strong influence on adult mass, the potential influence of other factors like the social environment or the prevalence of parasites or diseases on offspring growth, and growth canalisation, would require further investigations. In conclusion, our results suggest that since offspring reproductive success was independent from maternal investment, females should rather invest in offspring quantity rather than offspring quality.

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Influence of body mass on life history trajectories in wild house mice

To be submitted

Influence of body mass on life history trajectories in wild house mice

Yannick Auclair*, Barbara König & Anna K. Lindholm

Institute of Evolutionary Biology and Environmental Studies, University of Zurich, Winterthurerstrasse 190, CH-8057 Zurich, Switzerland

Abstract

Body size is probably one of the most important factors that determine individuals' fitness as shown by the ubiquity of its allometric relationships with life history traits such as the age at sexual maturity, brood size or survival. The influence of body mass on life history traits and life history trajectories has been studied in a number of species, but the most detailed mammalian studies are limited to ungulates. The large, long-lived and slow breeding ungulates however contrast with the majority of mammal species which are small, shorter-lived and have a rapid rate of reproduction. We addressed this gap using individual lifetime data from 384 free living house mice *Mus musculus domesticus* to test the effect of adult male and female body mass on their age at first reproduction, lifetime reproductive success and longevity, while controlling population density. Furthermore, we looked for sex-specific and alternative life history trajectories. Body mass did not predict individuals' lifetime reproductive success but the heaviest individuals reproduced earlier and had a shorter lifespan. Reproduction was deferred when population density increased, especially in males. Lifetime reproductive success, which was skewed in both sexes, increased with longevity. Males, who were heavier and had a shorter lifespan than females, showed three different life history trajectories which reach a fitness peak. The first consisted of an early reproduction and a very short lifespan whereas the second combined an early reproduction with a long lifespan, and the third associated a late reproduction with a medium longevity. Females showed only one fitness peak, at a life history trajectory combining a mid-age first reproduction with a long lifespan. In both sexes, life history trajectories were independent from body mass or population density. This study suggests that other factors like social competence may play a crucial role in determining individuals' lifetime fitness in species living in complex social societies like the house mouse.

Keywords: House mice – Body mass – Sexual dimorphism – Reproductive success – Longevity – Primiparity – Population density – Life history strategy

Introduction

Fitness is defined as the "average capacity of a phenotype to produce mature offspring relative to other individuals in the same population at the same time" (Danchin, Giraldeau & Cézilly 2008). In addition to natural selection that increases individuals' fitness by favouring traits improving predator/prey detection, fertility or immunity against pathogens, individuals' fitness can also be improved by traits that are chosen by sexual partners (selected through inter-sexual selection) or traits that improve their competitiveness against individuals of the same sex to access the gametes of the other sex (selected through intra-sexual selection). Body size is probably one of the most important factors that determine individuals' fitness as shown by the ubiquity of its allometric relationships with life history traits like the age at sexual maturity, brood size or survival (Blueweiss et al. 1978; Millar & Hickling 1991; Oli & Dobson 2003; Peters 1986). Moreover, body size has been shown to be closely associated with life history differences between populations of the same species (Reznick, Bryga & Endler 1990).

Body mass is under strong selection pressure in social species where reproduction is restricted to a few individuals who occupy the highest ranks along the dominance hierarchy. As dominance hierarchy is usually determined through the outcome of aggressive interactions, individuals relatively bigger than others have a higher chance to win fights and thus become dominant over same-sex individuals (Apollonio et al. 1992; Beaugrand, Payette & Goulet 1996; Klemme, Ylönen & Eccard 2007; Renison, Boersma & Martella 2002). Furthermore, the biggest individuals may also start to reproduce earlier than their smaller counterparts as they are more likely to successfully challenge dominant individuals soon after their sexual maturity. Although a large body size can favour the access to reproduction (Anderson & Fedak 1985; Oakeshott 1974) or increase brood size (Tuomi 1980), the costs of the repeated fights associated with the tenure of a breeding position may compromise survival. A shorter longevity would limit the number of reproductive events hence lifetime reproductive success (Bérubé, Festa-Bianchet & Jorgenson 1999; Pettorelli & Durant 2007; Weladji et al. 2006). The evolution of a trait allowing an early onset of reproduction, many reproductive events and prolonging longevity is therefore impossible because of the multiple trade-offs that exist between life history traits (Roff 2002; Stearns 1989, 1992). Consequently, only particular sets of life history traits are optimal.

Life history trajectories correspond to the different combinations of life history traits that can be observed in a given population in a given context (Stearns 1976). Alternative life history trajectories can evolve between populations of a same species in response to specific

circumstances. For instance, population density can deeply influence life history traits (Clutton-Brock 1988; Gaillard et al. 1997; Gilbert & Krebs 1991; Saitoh 1981). The number of competitors for limited resources like breeding sites or mating partners is lower in growing populations, or in populations under their carrying capacity, than in stable populations. An early onset of reproduction (Cole 1954; Lewontin 1965; Saitoh 1981) associated with a short survival (Gaillard et al. 1997; Jorgenson et al. 1993) may be the most successful strategy in a growing population whereas a deferred reproduction associated with a longer survival may be better in a stable population (Stearns 1976).

Alternative life history strategies can also evolve in the same population between or within individuals of the same sex (Gross 1996). For instance, male red deer *Cervus elaphus* are under a stronger intra-sexual selection than females which causes sex-specific reproductive strategies (Clutton-Brock & Guinness 1982). In coho salmon *Oncorhyncus kisutch*, males can either follow a "hooknose" or a "jack" strategy. Hooknose males are large and fight to access females whereas jack males are small and sneak to access females (Gross 1985). Although these strategies may show differences in the age at first reproduction or survival, their similar lifetime fitness explain their persistence in populations (Brockmann & Taborsky 2008; Gross 1985; Shuster & Wade 1991). Mammalian studies reporting the influence of body mass on life history traits and strategies are unfortunately limited to ungulates that are large, long-lived and slow breeding species (Clutton-Brock & Guinness 1982; Festa-Bianchet, Jorgenson & Réale 2000; Gaillard et al. 2000; Jorgenson et al. 1993).

The present study proposes to investigate the influence of body mass on lifetime fitness, measured as the age at first reproduction, the number of offspring weaned and longevity in a free-roaming population of house mice *Mus musculus domesticus*.

The house mouse is a small, short-lived mammal well known for its fast rate of reproduction favouring the quick colonization of new environments (Berry 1970; Brown 1953; Latham & Mason 2004). Breeding competition is high within both sexes and reproduction is skewed towards few individuals (DeFries & McClearn 1970; König & Lindholm 2012; Rusu & Krackow 2004). Aggressive interactions occur among both sexes to establish dominance relationships (Crowcroft & Rowe 1963; Krackow 1993). Males compete against each other to access females and control territories (Oakeshott 1974) whereas females compete against each other over the access to the best nest sites (Stockley & Bro-Jørgensen 2011; vom Saal et al. 1995). Female house mice are, however, expected to be more social than males as dominant females tolerate their subordinates better than dominant males tolerate theirs (Crowcroft 1955; Poole & Morgan 1976). Moreover, females are frequently observed

pooling their young in communal nests where they share maternal care (Auclair et al. 2014; Weidt, Lindholm & König 2014). These sex differences in social tendencies may contribute to the shorter male survival that has been observed in this species (Manser et al. 2011). The house mouse is therefore an ideal candidate to examine the influence of body mass on life history traits and possible sex-specific life history trajectories.

Material and methods

Study population

Data were collected from a free-living wild house mouse population in a $70m^2$ building in the vicinity of Zurich, Switzerland. Although mice can exit the building through several holes in the walls or under the roof, none of the mammalian or avian predators that occur outside can enter. The large permeability of the building towards mice does not allow the collection of emigration data. Water and food, a 50/50 mixture of oats and hamster food (Landi AG, Switzerland), were provided *ad libitum* to match conditions under which natural house mouse populations are observed (Berry 1970). The entire population was captured every seven weeks to estimate adult population density. Population density increased over time (König & Lindholm 2012). Additional details about this population can be found in König and Lindholm (2012) and Auclair et al. (2014).

Adult body mass

Individuals were weighed to the nearest 0.1g when the whole population was captured and considered adult whenever they weighed at least 16g (Berry 1981). At that time, individuals were injected with a sub-cutaneous transponder (RFID tag; Trovan® ID 100, 0.1 g weight, 11.5 mm length, 2.1 mm diameter) for later identification. Our experimental design did not allow for individual identification before adulthood, and it was impossible to weigh all individuals at the same age. Instead, results from the genetic identity analysis, which identified adults first found as pups, and which therefore had a known birthdate (see section below) had to be known to correct adult body mass for age (see results section).

Genotyping and genetic analysis

An ear tissue sample was collected on each pup when it was 13 days old. This is the closest age to weaning one can handle litters without causing too much disturbance as pups start to open their eyes and be mobile at 14 days of age (actual weaning occurs at 21-23 day old (König & Markl 1987)). Furthermore, an ear tissue sample was also collected from every

adult that was weighed and on all corpses found which did not carry a transponder. All genetic samples were genotyped at 25 microsatellite loci and a maximum likelihood parentage analysis was performed to a 95% level of confidence (see Auclair et al. 2014 for details). As pups were not individually marked, we used a genetic identity analysis to match genotypes of pups with those of adults sampled later. Genotypes at the same 25 microsatellite loci were used for an identity analysis in Cervus 3.0 (Kalinowski, Taper & Marshall 2007), allowing one allelic mismatch.

Lifetime fitness

A total of 384 individuals (167 females and 217 males) that were born between the 1st of January 2007 and the 31st of December 2009 from 211 litters produced by 124 mothers were used in this study. We measured their reproductive output as the number of offspring from each that survived until weaning (defined as those who reached 13 days of age) and as their age at first reproduction for the 219 individuals who did reproduce (100 females and 119 males). Furthermore, the detection of corpses allowed us to calculate longevity for 147 of these 384 individuals (56 females and 91 males). Overall, age at first reproduction, number of offspring weaned and longevity was available for 121 individuals (48 females and 73 males).

Offspring data and genetic samples were collected until the 31st of December 2012 to determine individuals' reproductive success and until the 30th of June 2013 to measure longevity. The latest detection of a living focal individual in the building was on February 21st 2012 and the last corpse was collected on March 26th 2012. Thus, the fitness estimates presented here can be considered as lifetime fitness data.

Statistical analyses

Statistical tests were carried out using R 3.0.2 (R Development Core Team 2013). Longevity and age at first reproduction were analysed with two independent linear models accounting for adult body mass, sex, population density, and their second degree interactions. Significance of the fixed effects was tested using F-tests. The same fixed effects structure was used in a zero inflated model fitted for a negative binomial distribution of the errors to analyse the lifetime reproductive success (Zeileis, Kleiber & Jackman 2008). A generalized linear model fitted for a quasi-poisson distribution of the errors was used to examine the covariation between the fitness estimates. This model allowed testing for the effect of the age at first reproduction, longevity, sex, and their second-degree interactions on the lifetime reproductive success. The age at first reproduction and longevity were accounted as second polynomial

terms in the model to correct for a possible curvilinear relationship with lifetime reproductive success. Significance of the fixed effects was given by *t*-tests. Adaptive landscapes of lifetime reproductive success in relation to the age at first reproduction and longevity were used to emphasize fitness peaks within each sex. A graphical inspection allowed determining fitness peaks whenever life reproductive success reached at least 15 pups. Then, we tested whether body mass or population density at birth of the individuals at the identified fitness peaks differed from the other individuals using Wilcoxon or Kruskal-Wallis tests when appropriate.

Results

Adult body mass

As individuals could not all be weighed at the same age, the measure of body mass had to be corrected for age. A negative exponential function was therefore fitted to the data and the residuals were used as a proxy for adult body mass in further analyses (Figure 1a). The analysis of these residuals showed a sexual dimorphism in adult body mass with males heavier than females (t-test: $t_{382} = -10.59$, $p < 0.001$; Figure 1b).

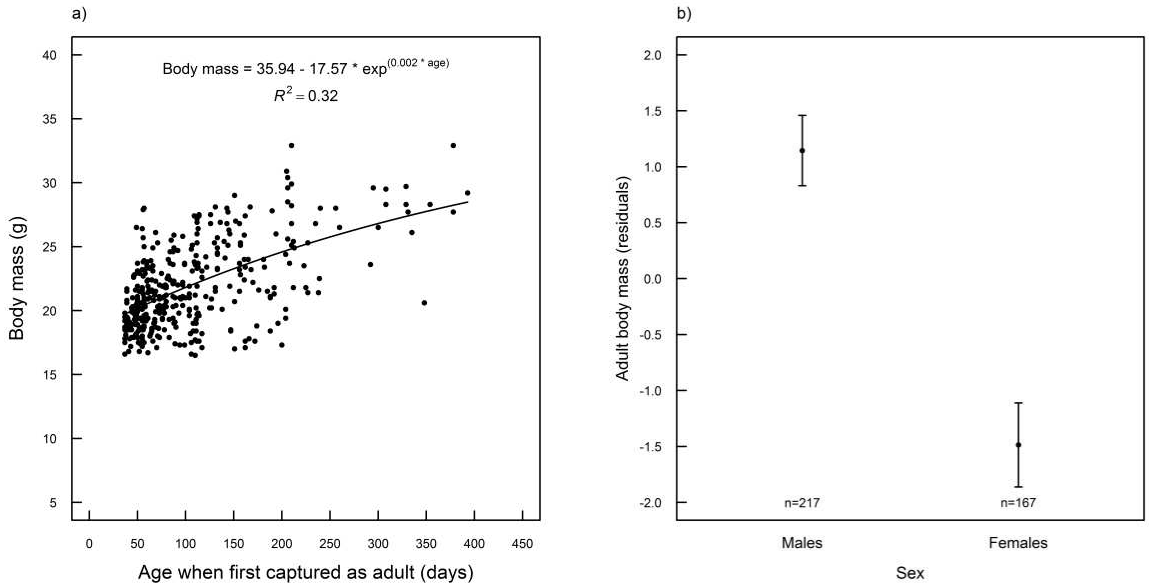

Figure 1. Residuals extracted from the negative exponential function of body mass against age in adults a) showed a sexual dimorphism b) (means ± 95% CI).

Lifetime fitness consequences of adult body mass

Individual lifetime reproductive success, as measured by the number of offspring weaned over a lifetime, was not significantly influenced by adult body mass, sex, population density or any of their second degree interactions (Table 1).

The age at first reproduction, however, was significantly influenced by adult body mass, the heaviest adults reproducing earlier (Table 1; Figure 2a). Moreover, population density also had a significant influence on the age at which the individuals started to reproduce (Table 1). An increase in population density delayed the first reproduction. This relationship tended to be stronger in males than in females as indicated by the significant interaction between population density and sex (Table 1; Figure 2b). Neither sex nor its interaction with adult body mass or the interaction between adult body mass and population density had a significant effect on the age at first reproduction (Table 1).

Longevity was significantly influenced by adult body mass, sex, and the interaction between population density and sex (Table 1). The heaviest individuals lived shorter (Figure 3a) and females lived longer than males (Figure 3b). Moreover, females lived longer when population increased whereas males' longevity slightly decreased (Figure 3c). Population density, its interaction with adult body mass, and the interaction between adult body mass and sex did not significantly influence longevity (Table 1).

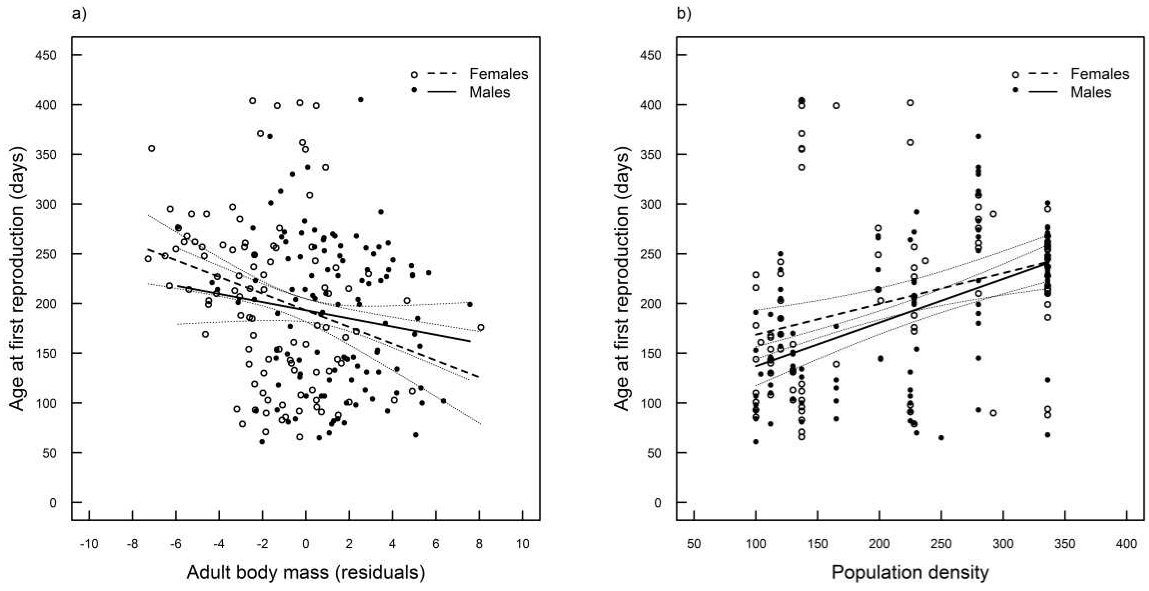

Figure 2. Influence of adult body mass a) and population density b) on the age at first reproduction within females and males (model predictions ± 95% CI).

Table 1. Influence of adult body mass, sex, and population density on individuals' fitness as measured by the age at first reproduction, number of offspring weaned, and longevity.

Fitness estimates	Explanatory variables	*F-test / Likelihood ratio test*	*p*
Lifetime reproductive success (# weaned offspring) N = 384	Body mass	$\chi^2 = 0.44$	0.506
	Sex	$\chi^2 = 0.28$	0.593
	Population density	$\chi^2 = 0.18$	0.670
	Body mass : Sex	$\chi^2 = 1.46$	0.227
	Body mass : Population density	$\chi^2 = 0.01$	0.998
	Sex : Population density	$\chi^2 = 0.30$	0.584
Age at first reproduction N = 219	**Body mass**	$\mathbf{F_{1,218} = 16.42}$	**<0.001**
	Sex	$F_{1,218} = 1.04$	0.310
	Population density	$\mathbf{F_{1,218} = 40.72}$	**<0.001**
	Body mass : Sex	$F_{1,218} = 0.23$	0.629
	Body mass : Population density	$F_{1,218} = 0.36$	0.550
	Sex : Population density	$\mathbf{F_{1,218} = 3.48}$	**0.063**
Longevity N = 147	**Body mass**	$\mathbf{F_{1,146} = 6.21}$	**0.014**
	Sex	$\mathbf{F_{1,146} = 36.84}$	**< 0.001**
	Population density	$F_{1,146} = 1.25$	0.266
	Body mass : Sex	$F_{1,146} = 3.08$	0.081
	Body mass : Population density	$F_{1,146} = 0.16$	0.690
	Sex : Population density	$\mathbf{F_{1,146} = 3.90}$	**0.050**

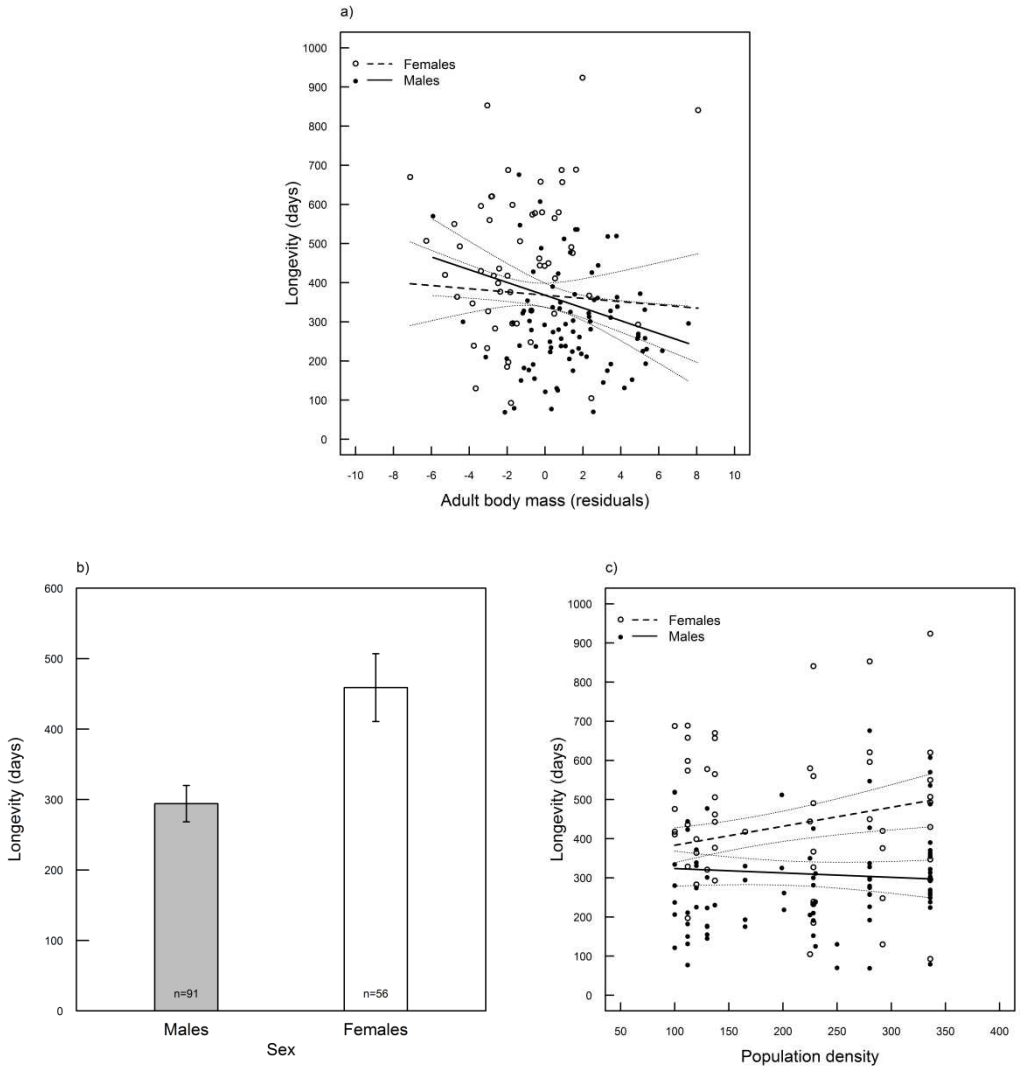

Figure 3. Influence of adult body mass a), sex b), and the interaction between population density and sex c) on longevity. Figure a) and c) show model predictions ± 95% CI while figure b) shows means ± 95%CI.

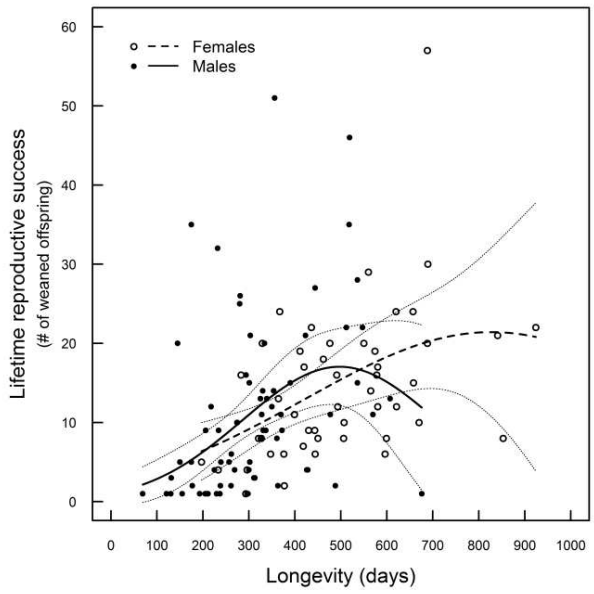

Figure 4. Positive relationship between longevity and lifetime reproductive success.

Covariation between life history traits

Individual reproductive success was significantly influenced by longevity and its quadratic term, indicating a curvilinear relationship (Table 2). Furthermore, the influence of longevity on lifetime reproductive success tended to interact with sex (Table 2). Overall, the longer individuals lived, the more offspring they produced (Figure 4). This positive relationship was stronger in males than in females but it started to plateau at 800 days in females whereas it plateaued and started decreasing at 500 days in males (Figure 4). The age at first reproduction, sex and all remaining second-degree interactions between longevity, age at first reproduction, and sex had no significant effect on individuals' lifetime reproductive success (Table 2).

Life history trajectories

Individual lifetime reproductive success showed a skew in favour of few individuals within each sex in our population (Figure 5). The adaptive landscape of lifetime reproductive success showed three different fitness peaks in males whereas there was only one in females (Figure 6). The first two peaks observed in males combined an early onset of reproduction around 100 days old with either a short longevity of about 180 days ("ES" trajectory) or a longer longevity of about 500 days ("EL" trajectory). The third peak was described by the association of a late first reproduction until males were approximately 225 days old with a medium longevity of about 350 days ("LM" trajectory). Among the 73 males for which measures on the three fitness estimates were available, 3 were in "ES" peak, 11 were in the "EL" peak and 5 were in the "LM" peak.

The unique fitness peak observable in females reflected a first reproduction at a medium age of 225 days old and a longevity of approximately 700 days (Figure 6). This fitness peak was reached by 9 of the 48 females for which measures on the three fitness estimates were available.

Factors influencing life history trajectories

There was no significant difference in the body mass (Kruskal-Wallis test: $\chi^2 = 1.27$, df = 3, $p = 0.737$; "ES" trajectory: 2.10 ± 0.49 residual body mass, "EL" trajectory: 1.59 ± 0.44 residual body mass, "LM" trajectory: 1.59 ± 0.40 residual body mass, other males: 1.20 ± 0.37 residual body mass) or population density at birth (Kruskal-Wallis test: $\chi^2 = 1.80$, df = 3, $p = 0.615$; "ES" males: 174 ± 29 individuals, "EL" males: 199 ± 31 individuals, "LM" males: 222 ± 51 individuals, other males: 228 ± 11 individuals) between the males who reached the three different fitness peaks and those who did not.

Table 2: Generalised linear modeling of the age at first reproduction, longevity, and their second-degree interactions on individuals' lifetime reproductive success.

Response variable	Explanatory variables	*Estimate [95%CI]*	*t*	*p*
Lifetime reproductive success (# weaned offspring) N = 121	Intercept	2.23 [1.87, 2.59]	12.06	<0.001
	Age at first reproduction	-1.74 [-4.80, 1.32]	-1.12	0.266
	Age at first reproduction^2	-1.65 [-4.35, 1.05]	-1.20	0.233
	Longevity	**6.49 [2.52, 10.45]**	**3.21**	**< 0.001**
	Longevity^2	**-2.62 [-5.21, -0.03]**	**-1.98**	**0.050**
	Sex	0.08 [-0.36, 0.52]	0.35	0.725
	Age at first reproduction x Longevity	0.70 [-1.65, 3.05]	0.59	0.558
	(Age at first reproduction x Longevity)^2	-0.50 [-2.99, 1.99]	-0.40	0.692
	Age at first reproduction x Sex	-3.29 [-7.59, 1.01]	-1.50	0.137
	Age at first reproduction^2 x Sex	0.97 [-3.20, 5.14]	0.46	0.649
	Longevity x Sex	-4.45 [-10.08, 0.22]	-1.68	0.096
	Longevity^2 x Sex	-4.77 [-9.64, 0.74]	-1.72	0.088

Neither body mass (Wilcoxon test: $W = 206$, $p = 0.435$; females at fitness peak: -0.87 ± 0.67 residual body mass, other females: -1.34 ± 0.46 residual body mass) nor population density at birth (Wilcoxon test: $W = 120.5$, $p = 0.147$; females at fitness peak: 174 ± 33 individuals, other females: 202 ± 14 individuals) were significantly different between the females who reached the fitness peak and those who did not.

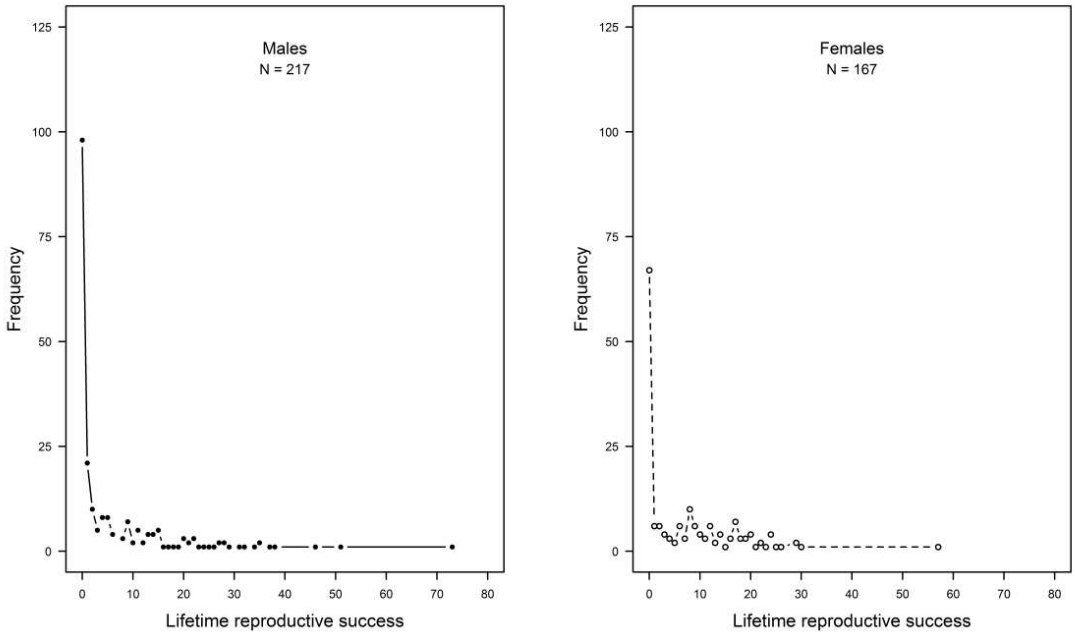

Figure 5. Reproductive skew in males and females.

Discussion

Despite having no direct effect on lifetime reproductive success, body mass influenced the onset of reproduction and longevity. Heavier individuals started to reproduce earlier, which may correlate with their likelihood to become dominant. Dominant positions are associated with a privileged access to reproduction in a wide range of species (white-toothed shrew *Crocidura russula* (Bouteiller-Reuter & Perrin 2005); grey-sided vole *Clethrionomys rufocanus* (Ims 1987); house mouse *Mus domesticus* (Singleton & Hay 1983); domestic cat *Felis* catus (Say, Pontier & Natoli 2001); bighorn sheep *Ovis canadensis* (Festa-Bianchet et al. 2000); red deer *Cervus elaphus* (Clutton-Brock, Albon & Guinness 1984); grey seal *Halichoerus grypus* (Anderson & Fedak 1985); savannah baboon *Papio cynocephalus* (Alberts, Watts & Altmann 2003)). In most cases, dominance hierarchy is established through the outcome of aggressive interactions in which relatively bigger individuals are more likely to win (Apollonio et al. 1992; Clutton-Brock et al. 1979; Clutton-Brock et al. 1988; Klemme et al. 2007).

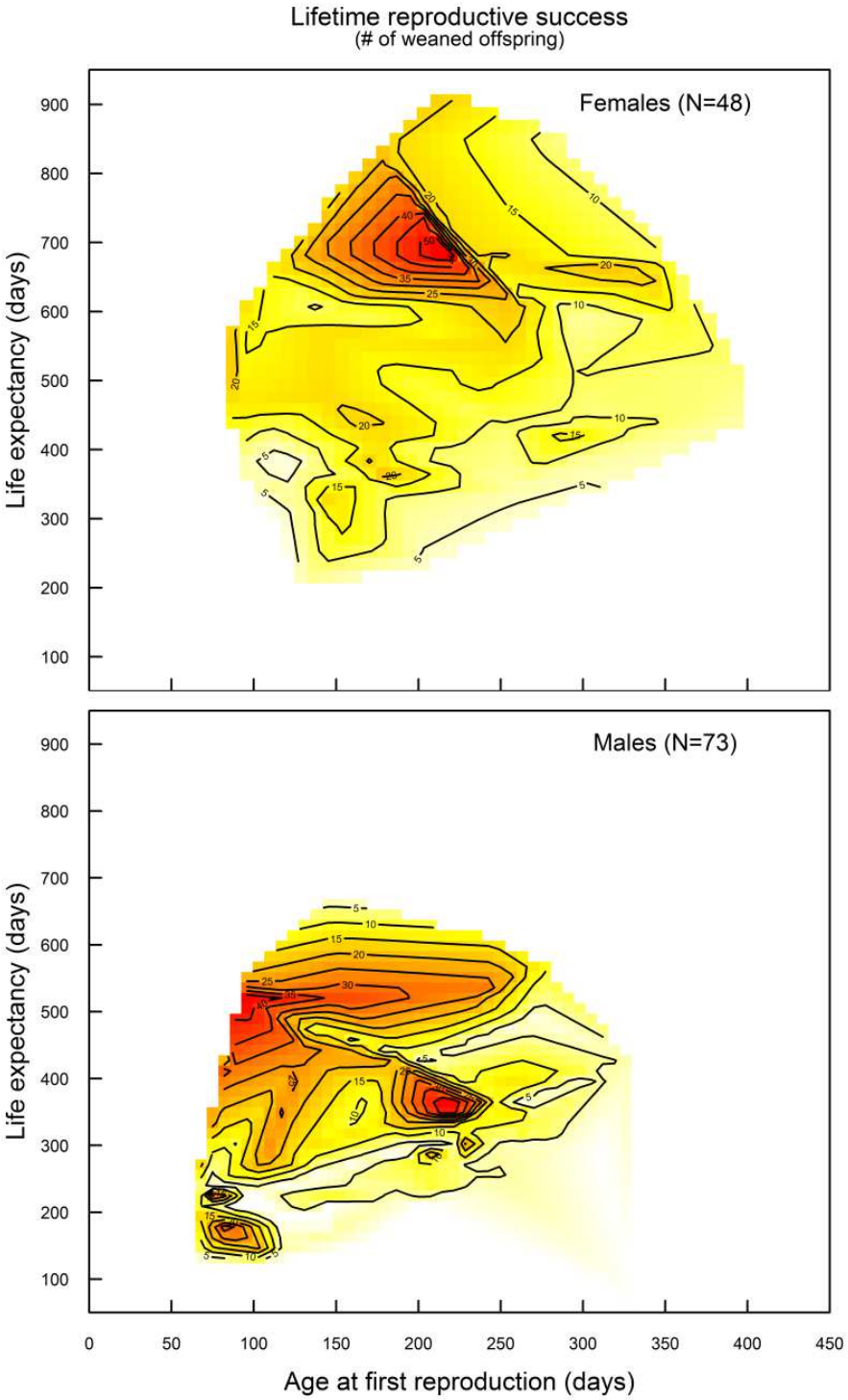

Figure 6. Adaptive landscapes for age at first reproduction and longevity in females and males. The fitness of individuals having a particular combination of these two traits is indicated by contours on the plot: the colour increases gradually from yellow to red with lifetime reproductive success.

As any trait closely associated with reproductive competition, body mass is under sexual selection. A sexual dimorphism can therefore evolve whenever a sex is under stronger selection pressures than the other (Klemme et al. 2007). Although males were heavier than females in our study, body mass predicted the age at first reproduction in both males and females suggesting that body mass was under intra-sexual selection in both sexes (Stockley & Bro-Jørgensen 2011). Similarly to what is commonly observed in males, reproduction can also be skewed toward dominant females (Clutton-Brock et al. 1984; Rusu & Krackow 2004). In this study we found high reproductive skew in both males and females. Female competition may occur to control territories housing the best nest sites or to control the access to food (Ostfeld 1985; Reimer & Petras 1967; Stockley & Bro-Jørgensen 2011; Wolff 1993). These two features are important to ensure a successful breeding by preventing infanticide or predation (Canali et al. 1991) and allowing sufficient energy intake to sustain the high costs of lactation (Hammond & Diamond 1992; König, Riester & Markl 1988).

The intensity of the breeding competition is density-dependent as the number of competitors over limited resources like nest sites, food or breeding territories increases with population density. Consequently, we observed that individuals had a later onset of reproduction when population density was higher. This result concurs with previous studies in house mice (Bronson 1979; Pelikán 1981), northern red-backed voles *Clethrionomys rutilus* and deer mice *Peromyscus maniculatus* (Gilbert & Krebs 1991), bighorn sheeps *Ovis Canadensis* (Jorgenson et al. 1993), and grey red-backed voles *Clethrionomys rufocanus bedfordiae* (Saitoh 1981). Small individuals, who are the least competitive, may choose to defer reproduction until the breeding competition becomes less intense or their competitiveness improves (Kokko & Johnstone 1999; Komers, Pélabon & Stenström 1997; van de Pol et al. 2007). Individuals can, however, benefit from doing so only when the costs of dispersal outweigh those of deferring reproduction (Batzli, Getz & Hurley 1977; Oli & Armitage 2003).

A competition over breeding generates different sources of stress which can have substantial effects on individuals' survival (Boonstra, McColl & Karels 2001; Boonstra 2005). For instance, large individuals may have to expose themselves to reproductive competition more often than their smaller counterparts. Large individuals are more likely to be dominant hence being at risk of injuries or death while fighting to maintain their dominant position. Moreover, dominant individuals seldom consider small individuals as a threat and attack them less frequently (Oakeshott 1974). This may explain why we found that the heaviest individuals had the shortest lifespan in the studied population. The longer survival of females

compared to males reported here could result from sex differences in how individuals compete against each other (Stockley, Bottell & Hurst 2013). Males may be subject to severe injuries or death more often than females due to repeated agonistic interactions with other males (Boonstra et al. 2001; Crowcroft & Rowe 1963; Hurst 1987; Reimer & Petras 1967; Singleton & Hay 1983). It has been proposed that dominant females are less often involved in fights against their subordinates than dominant males because, conversely to males, they can physiologically suppress them (Clutton-Brock et al. 1979; Clutton-Brock & Isvaran 2007; Clutton-Brock 2009). Differences in energy allocation strategies could also create gender differences in longevity. For instance, female house mice are less active than males and may allocate this spared energy to survival (Auclair, König & Lindholm 2013; Perrigo 1990). As house mice are income breeders, the costs of reproduction may have a strong effect on survival as reproduction occurs only when there is enough food available (Stearns 1992). The costs of reproduction may also be reduced by our experimental design which offered constant food availability (Metcalfe & Monaghan 2013).

Longevity was a strong predictor of lifetime reproductive success in the studied population (see also Bérubé et al. 1999; Pettorelli & Durant 2007). The conceptual idea behind this result is that a longer life gives an individual the opportunity to reproduce multiple times (Weladji et al. 2006). Conversely to what has been reported in other mammals, the number of offspring produced over a lifetime was not influenced by body mass, sex, population density or the age at first reproduction (Clutton-Brock 1988; Festa-Bianchet et al. 2000; Fuchs 1982; Millar 1977; Oli & Armitage 2003; Tuomi 1980). Although the age at first reproduction is an important component of fitness through the earlier contribution of the descendants to the genetic pool of a population (Cole 1954; Hamilton 1966; Lewontin 1965; Oli & Armitage 2003), it does not necessarily translate into a higher lifetime reproductive success.

Ideally, individuals should evolve traits that simultaneously favour an early onset of reproduction, a large number of offspring per reproductive event and a prolonged longevity. Such a scenario is unfortunately impossible because of the trade-offs existing between these life history traits (Helle & Lummaa 2013; Stearns 1989). Instead, particular combinations of life history traits called life history trajectories have been selected (Stearns 1976). Adaptive landscapes allows visualizing fitness peaks that correspond to these trajectories (Mangel 1991). Our study revealed that female and male house mice followed different life history trajectories leading to a similar reproductive success. These life history trajectories, however, differed in how they combined the age at first reproduction with longevity. Although we

detected only one trajectory leading to a fitness peak in females, there were three alternative high fitness trajectories in males. Females who reached the unique fitness peak had their first reproduction at approximately 200 days old, which corresponds to the average female lifespan in our population, and had a prolonged lifespan of about 650 days. The first two putative alternative life history trajectories followed by males consisted of an early reproduction at approximately 100 days old associated with either a short (ca. 180 days) or a long survival (ca. 500 days). The third male life history trajectory consisted of a late reproduction at approximately 200 days old and an average lifespan of 350 days.

The rise and persistence of alternative trajectories may be explained by the structure of the habitat, the intensity of the breeding competition or even female mate choice (Gage 1995; Stearns 1992; Warner 1984; York, Baird & Haynie 2014). Previous studies have already reported that small males may have to follow completely different strategies than bigger males to access reproduction (Feh 1999; Gross 1985). The largest males may be capable of obtaining a breeding position soon after their sexual maturity but the difficulty of retaining a dominant position may compromise their survival when confronted with aggressive contenders (Baker 1981; Poole & Morgan 1976). Conversely, smaller males who sneak copulations and avoid the costs associated with dominance can live longer and compensate for their lower success per reproductive event (Feh 1999). Moreover, although house mice can reproduce all year, reproduction is more intense in summer than in winter (König & Lindholm 2012; Latham & Mason 2004). These subsequent fluctuations in population density, hence in breeding competition, may alternatively favour different life history trajectories through disruptive selection. Within each sex, however, our results showed that body mass and population density had no significant effect on the life history trajectory individuals followed.

The coexistence of alternative male life history trajectories may be favoured by female mating behaviour (York et al. 2014). Female house mice have been shown to mate with multiple males (Dean, Ardlie & Nachman 2006; Firman & Simmons 2008; Manser et al. 2011). Females may seek genetic quality through their matings with big dominant males whereas matings with the small sneaky males may promote genetic compatibility and/or diversity (Hosken & Stockley 2003; Jennions & Petrie 2000; Parker & Birkhead 2013). Alternatively, female house mice have also been reported to mate with multiple males to avoid infanticide through paternity confusion (Auclair, König & Lindholm Accepted).

The late onset of reproduction and long lifespan specific to females may result from the evolution of social traits contributing to reduce the intra-sexual competition and the costs of deferring reproduction (Kokko & Johnstone 1999; Taborsky & Oliveira 2012). House mice

live in socially complex societies where social interactions between individuals are frequently observed (König & Lindholm 2012; Perony et al. 2012). Some "social abilities" improving the outcome of these repeated social interactions are therefore likely to have evolved (Oliveira 2009). This so-called social competence, as any performance trait, can be under natural selection since it shows inter-individual variation and there is growing evidence of its positive influence on Darwinian fitness (Oliveira 2009; Taborsky & Oliveira 2012). Socially competent individuals may be better at avoiding eviction by dominant individuals hence improving their survival and their opportunity to reproduce. A continuum in the social competence of individuals may thus lead them to follow alternative life history trajectories like those reported here within male house mice. The longer longevity of female house mice when population density increased compared to the slight decrease of the males suggests that females may be more socially competent than males in this species. Furthermore, female house mice are known to cooperate over maternal care in communal nests (Auclair et al. 2014; König 2006) and dominant females tolerate the presence of subordinates (Crowcroft 1955; Poole & Morgan 1976).

The present study showed in a small mammal where reproduction is highly skewed in both sexes that body mass did not predict lifetime reproductive success. Males and females who had a high reproductive success followed different life history trajectories independent of their body mass or population density. This suggests that other factors like social competence may play an important role in individuals' lifetime fitness in species living in socially complex societies like the house mouse.

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A selfish genetic element influencing longevity correlates with reactive behavioural traits in female house mice (*Mus domesticus*)

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A selfish genetic element influencing longevity correlates with reactive behavioural traits in female house mice (*Mus domesticus*)

Yannick Auclair*, Barbara König & Anna K. Lindholm

Institute of Evolutionary Biology and Environmental Studies, University of Zurich, Winterthurerstrasse 190, CH-8057 Zurich, Switzerland

Abstract

According to theory in life-history and animal personality, individuals with high fitness expectations should be risk-averse while individuals with low fitness expectations should be more bold. In female house mice, a selfish genetic element, the *t* haplotype, is associated with increased longevity under natural conditions, representing an appropriate case study to investigate this recent theory empirically. Following theory, females heterozygous for the t haplotype (+/*t*) are hypothesised to express more reactive personality traits and be more shy, less explorative and less active compared to the shorter-lived homozygous wildtype females (+/+). As males of different haplotype do not differ in survival, no similar pattern is expected. We tested these predictions by quantifying boldness, exploration, activity, and energetic intake in both +/*t* and +/+ mice. +/*t* females, unlike +/+ ones, expressed some reactive-like personality traits: +/*t* females were less active, less prone to form an exploratory routine and tended to ingest less food. Taken together these results suggest that differences in animal personality may contribute to the survival advantage observed in +/*t* females but fail to provide full empirical support for recent theory.

Keywords: Animal personality – Life-history – House mice – *t* complex – *t* haplotype – Activity

Introduction

In a wide range of taxa, it has been shown that individuals from the same population differ consistently in their behaviour. The concept of animal personality applies to behavioural differences that are consistent through time and situations (David, Auclair & Cézilly 2012; Réale et al. 2010a; Réale et al. 2007). Often, these behavioural traits are correlated within or across contexts and are referred to as behavioural syndromes (Bell 2007; David, Auclair & Cézilly 2011; Wilson et al. 2010). For instance, "proactive" individuals, in contrast to "reactive" individuals, have higher activity levels and a higher metabolic rate, are more exploratory and risk-prone (or bold), and faster to establish routines (Benus et al. 1990; Careau et al. 2009; Careau et al. 2008; Koolhaas et al. 1999; Marchetti & Drent 2000). How animal personalities evolved within populations still remains unclear, especially because behavioural plasticity could be seen as an optimal way to cope with fluctuating environments (Dall, Houston & McNamara 2004).

Life-history theory provides a framework for investigating the evolution of animal personalities (Biro & Stamps 2008; Stamps 2007; Wolf et al. 2007). Animal personality can have a profound influence on life-history traits like growth, fecundity and survival (Boon, Réale & Boutin 2008; Both et al. 2005; Stamps 2007). Using evolutionary models, Wolf and co-workers (Wolf et al. 2007) demonstrated that life-history tradeoffs promote the evolution of animal personalities. Individuals varying in exploration behaviour inhabited a low-quality resource habitat for a year at the end of which they could stay for a second year or move to a high-quality resource habitat. Superficial explorers, that evolved high levels of boldness in risky games (=proactive), invested more in current reproduction. Conversely, those that invested more in future reproduction were careful explorers, that evolved low levels of boldness in the same risky games (=reactive). These models therefore predict that individuals with different fitness expectations express different personality traits, here exploratory behaviour. The authors concluded that individuals with high expectations of future fitness, who have much to lose and for whom life is valuable, should be more cautious than individuals with low expectations.

Concurring with model predictions, recent evidence shows that individuals expressing reactive personality traits have a lower basal metabolic rate and therefore lower energetic needs (Careau et al. 2009; Careau et al. 2008). Metabolism of reactive individuals could allow them to survive longer by saving more energy than proactive individuals, especially when foraging involves risk-taking. For instance, a personality implying less risk-taking behaviour and conserving energy would favour survival (Boon et al. 2008; Clark 1994). Thus, long-lived

individuals should express a reactive-like personality whereas individuals characterized by a low life expectancy should express a proactive-like personality (Wolf et al. 2007).

The *t* haplotype, also called the "*t* complex", a naturally occurring genetic variant in the house mouse (*Mus domesticus*), provides an appropriate case study to investigate this hypothesis and hence fill the gap of empirical data. The *t* haplotype is a selfish genetic element, consisting of many linked genes, showing drive (Lyon 2003). Its main known fitness effect is a reduction in litter size in matings between heterozygotes due to a recessive lethal allele (Lenington 1991). Recently, *t* related effects on life-history have been documented. In a free-living population of house mice, female heterozygotes (+/*t*) live longer than homozygous wildtype females (+/+), with a 30% viability advantage (Manser et al. 2011). No difference in survival was found between +/+ and +/*t* males. Although no information is yet available on whether life expectancy positively correlates with fitness in wild house mice, mean life expectancy has been reported to be 100-150 days (Berry & Jakobson 1971; Pennycuik et al. 1986) whereas generation time is about 270 days (Manser 2009). This indicates that many mice die before they successfully reproduce, thus suggesting that a higher life expectancy could improve the chance to reproduce.

Following theory on the evolution of life-history and personality (Biro & Stamps 2008; Wolf et al. 2007), we hypothesize that reactive personality traits co-evolved with the *t* haplotype. We therefore assessed personality traits in mice of both sexes and genetic backgrounds. We predicted that +/*t* females, characterized by a high survival rate, should express "reactive-like" personality traits and therefore be more shy, less active and less explorative compared to +/+ females, characterized by a lower survival rate. Moreover, we compared the propensity of +/+ and +/*t* to form routine as it has been shown to reflect individuals' ability to use information on their environment and then adapt to its potential changes (Benus et al. 1990; Guillette et al. 2009; Marchetti & Drent 2000). House mice travel their territory daily, covering and marking the same routes repeatedly. Through these routines, mice acquire highly habitual responses, which they can perform rapidly and with minimal sensory input (Latham & Mason 2004). As proactive individuals form routines faster than reactive individuals, we expect +/+ females to form such routines faster than +/*t* females. Finally, as an index of energy intake we monitored food consumption, expecting that reactive individuals, here +/*t* females, ingest less food compared with proactive individuals, here +/+ females (Careau et al. 2009; Careau et al. 2008). No differences were expected between males of different haplotypes as they have a similar survival rate.

Methods

Ethics statement

Animal use and experimental design were approved by the Veterinary Office Zürich, Switzerland (Kantonales Veterinäramt Zürich, no. 97/2009).

Study subjects

We used 82 sexually mature but non-breeding house mice (more than six weeks old; mean age ± SE = 184 ± 10 days) which were laboratory born F2 and F3 descendants of wild-caught individuals from the same population in the vicinity of Zürich as the one in which longevity differences were reported (Manser et al. 2011). We tested a total of 41 females (20 were +/+ and 21 were +/*t*) and 41 males (20 were +/+ and 21 were +/*t*) randomly selected from offspring of our breeding stock. No significant difference in age was observed between +/+ and +/*t* mice of the same sex (females: $t_{39} = 0.03$, $p = 0.973$; males: $t_{39} = 0.84$, $p = 0.408$). Males were younger than females ($t_{80} = 4.02$, $p < 0.001$), because high aggression among males meant that they could not long be housed in groups. All individuals were in good condition for the entire duration of the study.

Housing

All mice were singly housed in Macrolon Type II cages (267 x 207 x 140 mm), beginning 5 days before the first behavioural test. Each cage contained standard animal bedding (Lignocel Hygienic Animal Bedding, JRS), an empty toilet paper roll and some paper towel as hides and nest building material. Food (laboratory animal diet for mice, Provimi Kliba SA, Kaiseraugst, Switzerland) and water were provided ad libitum. Animals were kept under standardized laboratory conditions at a temperature of 22°C ± 3°C with a relative humidity of 50-60% and on a 14:10 light:dark cycle with a 1h sunrise and dusk phase at the beginning and end of the light phase.

Body weight

Mice were weighed twice at a 7-day interval with the first measurement the day before the first behavioural test and the second on the day following the end of the first series of behavioural tests. We did not observe significant changes in body weight ($t_{81} = 1.69$, $p = 0.095$). As the two measurements were highly repeatable ($R = 0.95$, $F_{81,82} = 40.52$, $p < 0.001$), we used the mean.

Genotype determination

An individual ear tissue sample was collected from all males and females at least one week before testing. DNA was isolated and amplified at the Hba-ps4 locus, a marker containing a 16-bp *t* haplotype specific insertion (Hammer, Schimenti & Silver 1989). PCR products were electrophoresed using an ABI 3730x1 and visualized using Genemapper 4.0 software (Applied Biosystems) to determine genotype at the *t* locus.

Schedule for the assessment of personality traits

For breeding convenience this study was realized in two sessions. The first session took place in February – March whereas the second session took place in July – August. Each behavioural test was performed twice with a seven day interval to check for individual consistency through time (Carere, Drent & Privitera 2005; Réale et al. 2000; van Oers et al. 2004). Exploration tests were however replicated after nine days because of a time constraint. Activity and boldness tests were performed in the morning (from 8:00 to 11:00), whereas the first assessment of exploratory behaviour was performed in the afternoon (15:00 to 18:00) and the replicate in the morning. All behaviour tests lasted ten minutes, with the observer standing immobile at a one meter distance. As the activity and boldness tests were performed using the home cage of the mice, the stress induced by the procedures was very limited. Within a three minute acclimation period the mice were very calm and were observed grooming themselves. A single mouse was involved in only one experiment per day and had one day free after each behavioural test. The behavioural tests were run blindly with regard to the genotype of the mice.

Activity

To measure individual activity, we removed nest material and the paper roll from the home cage to facilitate observations. We replaced the cage lid by a Plexiglas lid with a grid drawn on it to uniformly split the cage widthwise into three equal parts. After a three minute acclimation period, the observer recorded the number of times a mouse crossed the lines with all four paws for ten minutes. We then calculated an activity score following previous common procedures (Bell 2005; Quinn & Cresswell 2005).

Exploration

Exploratory behaviour was assessed in a concentric square field cage representing an arena composed of nine compartments, a central part surrounded by four corridors joined

alternatively by covered and uncovered corners (Augustsson & Meyerson 2004; Marques et al. 2008) (Figure 1). After each trial, the apparatus was cleaned with acetone to remove scent marks (Hurst 1989). A focal mouse was transferred in a small dark box from its home cage to the apparatus to reduce stress before the beginning of the test. The door of the box was aimed at the direction of a covered corner in the first trial and at the direction of an uncovered corner in the replicate. The sliding door of the box was opened by remote control (using a string), and latency time to leave the box, time needed to enter each compartment, and total number of visits to compartments were recorded. For convenience latencies were subtracted from the total duration of the test (600 seconds) such that highly explorative individuals, characterized by short latencies, received a high value.

Boldness

Boldness was assessed in a classical olfactory test realized with three Macrolon type II cages connected by tubes (Lenington, Egid & Williams 1988; Nunes, Maria da Luz & Ganem 2009). We connected a central cage to two cages, one at each side. The central cage was filled with bedding from the home cage of the individual tested. The two other cages were filled with either unused cat bedding for one or with soiled cat bedding for the other (Cat's Best Öko Plus, Qualipet). The soiled cat bedding had been used by a domestic cat during one week before the experiment. Cats represent a natural predator against which mice should have evolved avoidance mechanisms (Berry 1970; Dickman 1992). Following Dickman & Doncaster (Dickman & Doncaster 1984), mice should be able to assess the presence of predators indirectly through olfactory cues and avoid areas with predator's faeces or urine. Our setting thus represents two identical areas, one of which has apparently been visited by a natural predator, allowing a test of boldness in the face of predator cues (Jedrzejewski, Rychlik & Jedrzejewska 1993; Lima & Dill 1990; Pillay, Alexander & Lazenby 2003). This procedure avoids a repeated exposure to a real predator, known to be highly stressful for mice (Marques et al. 2008).

Focal individuals were released in the central cage and kept there for a three minute acclimation period. Removable wire mesh partitions closed the tubes, allowing odour identification of the neighbour cages. At the start of the trial, partitions were removed and the time spent and the number of visits to each cage containing each type of cat bedding were recorded for ten minutes. The mice gave significantly more visits to (t_{81} = -3.25, p = 0.002) and spent significantly more time (t_{81} = -2.88, p = 0.005) in the cage filled with unused cat bedding than in the cage filled with soiled cat bedding.

Propensity to form routine

Routine formation is usually measured by changing a familiar environment that has been experienced repeatedly and subsequently testing how quickly individuals react to this environmental change (Benus et al. 1990; Benus, Koolhaas & van Oortmerssen 1987; Marchetti & Drent 2000). The propensity to form routine can be indirectly measured by the magnitude of the increase in the performance of a given behaviour between the replicated trials of the same test. Following this idea, we quantified the propensity to form routine as the difference between the performance measured at the second trial and the performance measured at the first trial.

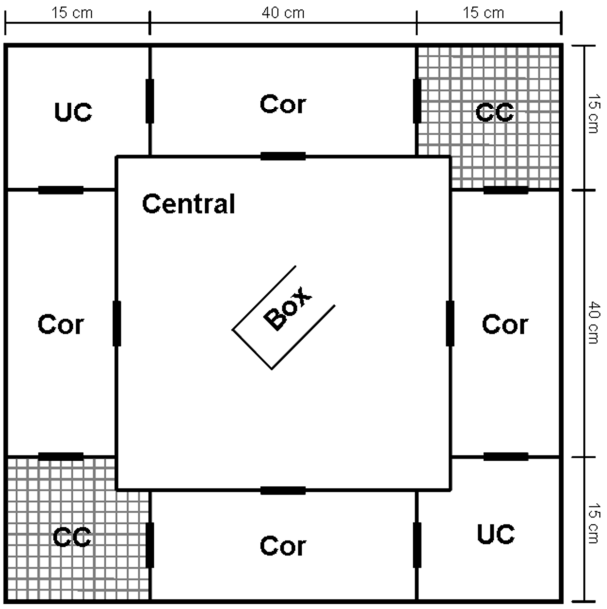

Figure 1. Concentric square field cage to test exploratory behaviour. CC = Covered Corners; Cor = Corridors; UC = Uncovered Corners; Central = Central Compartment; Box = dark box in which mice were transferred to the experimental cage. The holes, drawn in bold in the figure, that connect corridors with corners are 10 cm above the ground whereas the holes that connect the central area with the corridors are 1.5 cm above the ground.

Food consumption

Food consumption was only recorded for the 48 mice taking part in the second session because of a time constraint at the end of the first session. This sub-sample was composed of 23 females (12 +/*t* and 11 +/+) and 25 males (9 +/*t* and 16 +/+). During two consecutive weeks, one month after all behavioural experiments were carried out, the quantity of pellets eaten by the mice was recorded at the same time of day. On day 1 the food holder was cleaned and filled with new pellets of known quantity (weighed on an electronic balance, Sartorius BL 1500 S, with 0.01 g. precision). At day 7 and 14, uneaten pellets were removed for weighing,

and at day 7 replaced with new pellets. We checked daily if pieces of pellets had fallen through the feeder grid into the bedding. When found, they were removed and weighed. Food consumption was repeatable between the two weeks (intra-class correlation coefficient: $R = 0.44$, $F_{47,48} = 2.55$, $p < 0.001$).

Statistical analyses

Statistical tests were carried out using R version 2.13.1 (R Development Core Team 2012). Numbers of visits in the cage containing soiled cat bedding, number of visits in the cage containing clean cat bedding, and total number of visits in all compartments of the exploration apparatus test were square-root transformed, while activity scores, the time needed to explore all the compartments in the exploration test, and quantity of food eaten were log-transformed to satisfy normality.

We tested the influence of individual identity, the genetic background, sex, body weight, session and trial on the variables measured using linear mixed effect models. Interactions between genetic background and sex, trial and sex, trial and genetic background, and between trial, genetic background and sex were also included.

Individual identity was defined as a random effect to assess individual consistency (repeatability) while all other variables were defined as fixed effects. Significance of the random effect was determined by likelihood ratio tests while fixed effects were tested using *F* tests (Crawley 2007). We also used ANOVA-based intra-class correlation coefficients (*R*) to quantify individual consistency between the two trials of each behavioural test (Lessells & Boag 1987; Nakagawa & Schielzeth 2010). A significant effect of trial in the mixed effect models described above revealed a propensity to form routine. Potential effects of genetic background, sex or their interaction on routine formation were therefore assessed by the effect of the interactions involving trial in the same mixed effect models.

Multiple correlations between the personality traits showing individual consistency enabled us to check for correlations between personality traits. To avoid type I errors, we followed the Benjamini & Hochberg procedure that also reduced type II errors by controlling false discovery rate (Benjamini & Hochberg 1995; Verhoeven et al. 2005). Beforehand, the number of movements in the activity test, total number of visits to compartments in the exploration test, and the number of visits to cages containing clean and soiled cat bedding were averaged and then standardized (for each session separately) to control for the "session" effect found in the mixed effect models. For each trial the standardized variables are thus defined by an identical mean (equal to 0) and standard deviation (equal to 1).

Food consumption (total food consumed over two weeks) was normally distributed and was analysed using a general linear model to determine the influence of the genetic background, sex, body weight and their interactions. Non-significant interactions ($p < 0.05$) were dropped from the full model by a backwards stepwise procedure, following Crawley (Crawley 2007).

Results

Individual consistency

The number of movements during the activity test, the total number of visits to and the time needed to explore all the compartments in the exploration test, and the numbers of visits to the cage containing soiled cat bedding during boldness tests were consistent within an individual through time (Table 1). These variables were therefore used to test for behavioural syndromes.

Table 1. Individual consistency of the behavioural variables assessed twice at a one-week interval, estimated firstly from mixed model analysis accounting for genetic background, body weight, sex, session, trial and interactions, and secondly from ANOVA-based intra-class correlation coefficients.

Personality traits	Parameters	ID as a random effect		Intra-class correlation coefficients		
		Likelihood ratio	*p*	*R*	$F_{81,82}$	*p*
Activity	number of movements	36.05	<0.0001	0.73	6.49	<0.001
Boldness	number of visits to soiled cat bedding	7.36	0.007	0.31	1.91	0.002
	time spent in soiled cat bedding	0.01	0.999	−0.08	0.85	0.759
Exploration	total number of visits in compartments	23.49	<0.0001	0.43	2.53	<0.001
	time needed to visit all compartments	23.94	<0.0001	0.48	2.82	<0.001

Personality traits

The analyses of the influence of the genetic background, sex, and body weight on the personality traits showed that both the *t* haplotype, sex and their interaction had a significant effect on basic activity (Table 2). +/*t* females were less active than +/+ females, and females were in general more active than males (Figure 2). None of the personality traits measured in the boldness and exploration tests were influenced by the genetic background, sex or their interaction (Table 2). Body weight did not have any significant effect in any of the personality traits except for the total number of visits in the exploration test (Table 2).

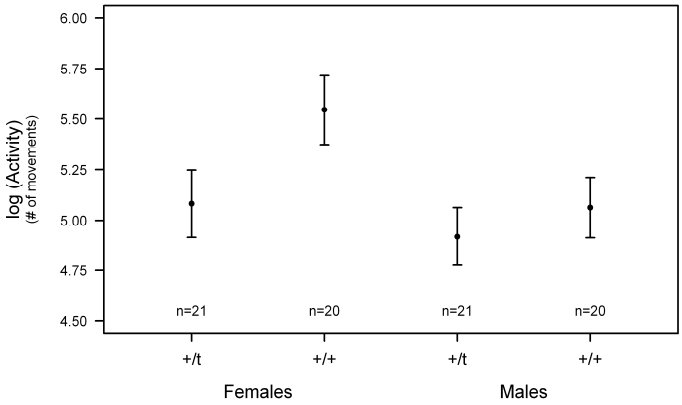

Figure 2. Effect of the genetic background and sex on activity score (mean ± standard errors predicted by mixed effect model).

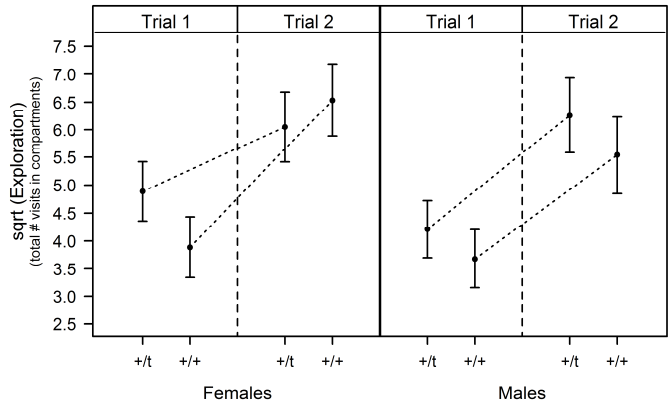

Figure 3. Effect of genetic background and sex on the propensity to form an exploratory routine: increase in exploratory behaviour (total number of visits to all compartments of the exploration apparatus) between the two trials (mean ± standard errors predicted by mixed effect model).

Propensity to form routine

No propensity to form routine was observed in the activity test as mice showed similar activity scores between the first and the second trial (Table 2). However, during the boldness test the number of visits increased during the second trial to both the cage with soiled cat bedding (1^{st} trial (mean ± SE): 5.5 ± 0.6, 2^{nd} trial: 8.4 ± 0.6) and the cage with clean cat bedding (1^{st} trial (mean ± SE): 6.6 ± 0.6, 2^{nd} trial: 9.0 ± 0.6) (Table 2). During the exploration test, the total number of visits to the compartments increased between the first and the second trial (1^{st} trial: 23.1 ± 2.7, 2^{nd} trial: 45.9 ± 4.8) whereas the time needed to explore all the compartments decreased (1^{st} trial: 560 ± 12 sec., 2^{nd} trial: 468 ± 22 sec.), both suggesting a propensity to form an exploratory routine (Table 2).

Genetic background, sex or their interaction did not have any significant influence on the propensity to form a routine observed in the boldness test, as measured by the number of

visits to the cage containing soiled cat bedding or the number of visits to the cage containing clean cat bedding (Table 2). The analysis of the propensity to form an exploratory routine as measured by the increase in the total number of visits in the exploration test did not show an overall influence of sex or genetic background but a significant effect of the interaction of genetic background with sex (Table 2). Heterozygous +/*t* females were less prone to form an exploratory routine than +/+ females as they had a lower increase in their number of visits whereas there was no significant difference between +/*t* and +/+ males (Figure 3). When analysing the decrease in the time needed to visit all the compartments between the two replicates, sex, genetic background or their interaction did not show any significant effect on the formation of an exploratory routine (Table 2).

Table 2. Mixed model analysis of the personality traits showing individual consistency.

	Personality traits							
	Activity		**Boldness**		**Exploration**			
	# movements		**# visits to soiled bedding**		**# visits in compartments**		**time needed to visit compartments**	
	F	*p*	*F*	*p*	*F*	*p*	*F*	*p*
Genetic background	5.37	0.023	0.03	0.853	1.76	0.188	0.21	0.650
Sex	5.88	0.018	1.91	0.171	1.14	0.289	0.42	0.517
Body weight	2.69	0.105	0.94	0.337	5.58	0.021	0.04	0.847
Session	30.21	<0.001	27.40	<0.001	78.23	<0.001	0.11	0.739
Trial	1.10	0.298	25.31	<0.001	75.77	<0.001	29.68	<0.001
Genetic background : Sex	5.20	0.025	0.09	0.770	1.04	0.312	2.51	0.118
Sex : Trial	0.07	0.787	0.10	0.754	0.02	0.876	0.78	0.380
Genetic background : Trial	0.02	0.877	1.40	0.241	0.66	0.418	0.02	0.881
Genetic background : Sex : Trial	0.18	0.671	1.12	0.293	6.52	0.013	0.29	0.592

Correlations between personality traits

The positive relationship between boldness and activity allowed us to define a behavioural syndrome in females but not in males (Table 3). More precisely, this relationship was significant in +/+ females whereas +/*t* females only showed a non-significant tendency to express it (Figure 4; Table 3).

Table 3. Correlations between personality traits showing individual consistency.

				Males						**Females**					
Behaviour pairs		**All individuals**		**All genotypes**		**+/+**		**+/*t***		**All genotypes**		**+/+**		**+/*t***	
		Pearson r	*p*	*Pearson r*	*p*	*Pearson r*	*p*	*Pearson r*	*p*	*Pearson r*	*p*	*Pearson r*	*p*	*Pearson r*	*p*
Boldness × Activity	# visits cat bedding × # movements	**0.31**	**0.005**	0.06	0.716	0.26	0.259	−0.23	0.312	**0.47**	**0.002**	**0.62**	**0.004**	0.37	0.101
Boldness × Exploration	# visits cat bedding × # visits	0.19	0.080	0.30	0.059	0.45	0.047	0.11	0.643	0.07	0.649	0.16	0.512	0.03	0.882
Activity × Exploration	# movements × # visits	0.16	0.147	0.14	0.383	0.35	0.131	0.05	0.831	0.14	0.396	0.26	0.274	0.07	0.763

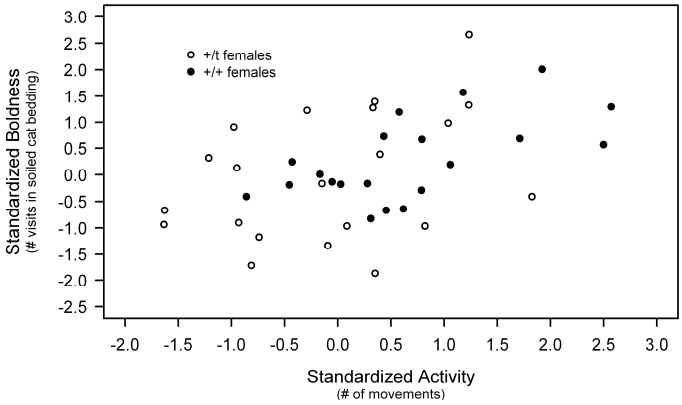

Figure 4. Activity - Boldness syndrome in females, according to genetic background.

Food consumption

Even though genetic background ($F_{1,46} = 0.12$, $p = 0.73$), sex ($F_{1,45} = 3.05$, $p = 0.09$), and body weight ($F_{1,44} = 2.56$, $p = 0.12$) did not show an overall influence on food consumption, the interaction between genetic background and sex had a marginally significant effect ($F_{1,43} = 3.72$, $p = 0.06$). Whereas +/+ males ate less than +/*t* males (+/+ males: 69.01 ± 3.79 g., +/*t* males: 76.95 ± 6.23 g.), the opposite was true in females, as +/*t* females ate less than +/+ females (+/*t* females: 61.02 ± 2.59 g., +/+ females: 68.27 ± 2.88 g.; Figure 5).

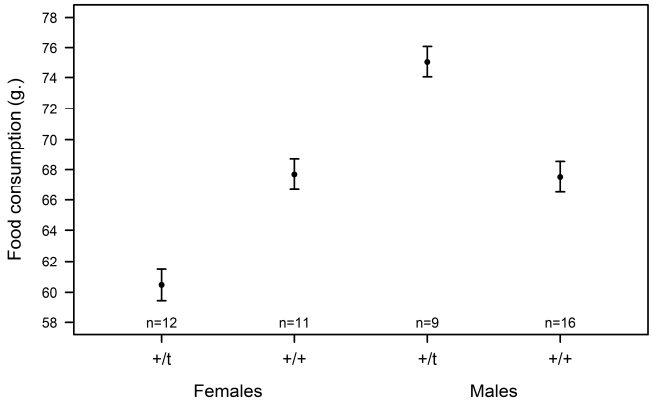

Figure 5. Influence of genetic background and sex on food consumption controlled for body weight (mean ± standard errors predicted by linear regression model).

Discussion

Our study demonstrated that laboratory reared female house mice of a genotype conferring a survival advantage under natural conditions expressed reactive-like behavioural traits favouring cautiousness and energy conservation. The longer living +/*t* females were less

active, less prone to form an exploratory routine, and tended to ingest less food than the shorter living +/+ females.

Having a low activity level could have various positive effects on survival. First, decreasing activity can be beneficial for small rodents when facing predators relying on hearing or sight to detect prey (Apfelbach et al. 2005). Second, organismal maintenance requires partitioning of the available energy budget to different biological functions among which effector organs like skeletal muscles are responsible for much of the daily energy expenditure (Ricklefs, Konarzewski & Daan 1996). Within a given energy budget, an individual with a reduced activity can attribute a large part of its energy budget to other functions that could improve survival.

Our results on food consumption supported our energy-saving interpretation as +/*t* females showed a tendency to have a lower food intake than +/+ females. This could reflect a lower need for energy and/or a better capacity to save energy that could both favour survival when access to food is restricted or risky. Our results suggest that reactive individuals could decrease the frequency of their visits to feeding places compared to proactive individuals and may decrease the risk of being caught by predators when feeding. Moreover, research on rate of aging in rodents showed that mice fed with a 65% reduced diet improve their maximum life span by 51% compared to mice fed *ad libitum* (Weindruch et al. 1986). Caloric restriction extends life span through mechanisms such as reduced oxidative damage (Mattson 2005). This could also apply to +/*t* females and hence would partly explain their survival advantage over +/+ females that have a higher food consumption.

Moreover, +/*t* females were less prone to form an exploratory routine. Although reactive and proactive individuals have similar learning abilities, at least in birds, reactive individuals form routines slower than proactive individuals (Guillette et al. 2009; Marchetti & Drent 2000). This particularity, seen as a higher attentiveness to the environment, confers an advantage to reactive individuals as they can better adjust to sudden environmental changes than proactive individuals (Benus et al. 1990; Exnerová et al. 2010; Guillette et al. 2011).

Conversely to other personality studies, we did not observe behavioural syndromes between most of the personality traits we assessed (David et al. 2011; Wilson et al. 2010). We found a syndrome defined by a positive correlation between activity and boldness, such that the less active females were also the more cautious. However, this relationship was significant in +/+ females whereas +/*t* females only showed a tendency. Some studies have shown that behavioural syndromes are not ubiquitous, even within the same species. In three-spined sticklebacks (*Gasterosteus aculeatus*) the presence of behavioural syndromes depends on

whether population characteristics favour suites of correlated behaviours (Bell 2005; Bell & Sih 2007; Dingemanse et al. 2007). The absence of behavioural syndromes in male house mice could thus be due to sex-specific behavioural optima.

The differences observed in the activity test are consistent with expected differences in energy demands due to milk production. Costs of lactation are very high in small rodents and increase with litter size (König, Riester & Markl 1988). Litter size is influenced by the *t* haplotype. On average +/*t* females have smaller litters than +/+ females, as whenever +/*t* females mate with +/*t* males their litter sizes are nearly halved due to the lethal homozygous effect of the *t* haplotype (Lindholm et al. 2013). Thus a female's expected average litter size should correlate with activity levels. Higher activity levels help to gather information about food to cover energetic needs during lactation. Consistent with this, we showed for non-breeding mice that +/*t* females had lower activity levels than did +/+ females. Fitness of +/*t* and +/+ females will on average be equal if +/*t* females compensate for smaller litters by producing more litters, which greater longevity would permit. This would contribute to maintaining the polymorphism in the population. Perrigo (1990) showed that lactation strongly influences activity patterns of females, and that males were less active than females. We also found that males were less active than females.

The lack of difference in exploration and boldness between mice of different sexes and genotype suggests that balancing selection has resulted in a single optimal behavioural level for each, with no correlation between individual values for each traits. House mice in western Europe live commensally with humans and nearly always are found close to easily accessible food resources, and often in dense population (Berry 1970; Latham & Mason 2004), suggesting that exploration to find new food patches may often be secondary to exploration to monitor social situations. Both males and females monitor the presence of conspecifics and defend their territories against intruders (Gray, Plesner Jensen & Hurst 2000). Similarly, boldness behaviour might be under strong balancing selection pressure reducing inter-individual variability, the raw material needed to evolve personalities.

Although our study provides interesting insights into personality traits associated with +/*t* females and survival differences, the causal relationship is unclear. The *t* haplotype, consisting of a third of chromosome 17, has had an independent evolutionary history from its wildtype counterpart for more than two million years (Morita et al. 1992). Major Histocompatibility Complex genes are located within the four inversions comprising the *t* haplotype (Hammerberg & Klein 1975) and there is evidence that a gene influencing both male and female mate choice is also located within the *t* haplotype (Lenington 1991). Genes

influencing other traits, such as personality and/or survival, either additively or epistatically or through dominance, could be located within this region.

Behavioural studies like ours do not only help in understanding the *t* haplotype but also underline new questions related to life-history trade-offs and the evolution of animal personalities (Biro & Stamps 2008; Réale et al. 2010b; Wolf et al. 2007). The rate-of-living theory postulates a negative association between life span and the rate of energy expenditure (Speakman et al. 2002). Thus two opposite strategies "live fast and die young" or "live slowly and die old", define a fast-slow life-history continuum along which individuals can be ranked (Bielby et al. 2007; Gaillard et al. 1989; Kraus et al. 2005). Our results give evidence that these two life-history strategies apply to the *t* complex, with +/+ females living extravagantly and +/*t* females living frugally. However, Wolf et al. (Wolf et al. 2007) predicted an association between residual reproductive value and risk-related behaviours like exploration or boldness so that we could expect +/*t* females to be shyer and less explorative than +/+ females. However, our results fail to provide full empirical support to theory as only activity showed a clear association with the *t* haplotype and we did not find a strong relationship between activity and boldness.

Literature provides few examples reporting the influence of personality traits like activity, aggressiveness, and sociality on reproductive success or longevity (Boon, Réale & Boutin 2007; Cote, Dreiss & Clobert 2008; Réale et al. 2009) (see (Smith & Blumstein 2008) for a review). Our study indicates that longer living house mice express reactive personality traits, demonstrating that longevity correlates with personality. However, as studies focusing on life-history productivity and personality are still missing in this species, we do not know if the expression of specific personality traits could also influence their reproductive success and/or tactics (Biro & Stamps 2008; Réale et al. 2010b).

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CONCLUSIONS AND OUTLOOK

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The aim of my thesis was to examine the fitness consequences of inter-individual differences in maternal behaviour, body mass or personality traits in wild house mice. I showed that females nesting communally rather than solitarily can reduce their maternal load through a reduction of their nest attendance and also improve their offspring survival by confusing the paternity of individual pups within the combined litters. Furthermore, I demonstrated that a higher postpartum maternal investment, leading to heavier offspring at weaning, does not increase offspring lifetime fitness. I found that, conversely to body mass at weaning, adult body mass predicts life history traits such as the onset of reproduction and longevity. Last, I showed that these longevity differences could also be explained by inter-individual differences in behavioural tendencies saving energy and favouring cautiousness.

In this final chapter, I will bring these different aspects together within the context of sociality. First, I will emphasize the fitness consequences of sociality. Second, I will highlight the importance of social partner choice in cooperative parental care. Finally, I will discuss the role that an early social environment could play on individuals' life history.

Fitness consequences of maternal competence in social interactions

Sociality occurs whenever individuals associate with conspecifics and live in communities in which social interactions are frequent (East & Hofer 2010; Krause & Ruxton 2002). The social environment of such species can be complex and highly variable over time so that natural selection may have favoured the evolution of some "social abilities" to perform better during social interactions (Oliveira 2009). Social competence has recently been defined as "the ability of an individual to optimize the expression of its social behaviour as a function of the available social information" (Taborsky & Oliveira 2012). It is now assumed that social competence, as any performance trait, can be under natural selection since it shows inter-individual variation and there is growing evidence of its positive influence on Darwinian fitness (Oliveira 2009; Taborsky & Oliveira 2012; West-Eberhard 1979).

Although social competence has been reported in a wide range of taxa and contexts in the laboratory, competence in social interactions has rarely been linked to fitness outcomes in the wild. However, a few studies have examined the fitness consequences of social bonding on survival or reproductive success. For instance, the early formation of social bonds improves male survival in bottlenose dolphins *Tursiops* sp., and female crested macaques *Macaca nigra* live longer when they have strong and stable bonds (Silk et al. 2010; Stanton & Mann 2012). In the yellow-bellied marmot *Marmota flaviventris*, the most social females

produced more yearlings and female recruits whereas assamese macaque *Macaca assamensis* males improve their chance of siring offspring when they bond to each other to form coalitions (Armitage 1986; Schülke et al. 2010).

Social bonding can also contribute to improving individuals' reproductive success by enhancing offspring survival. Female assamese macaques establish strong bonds with males that could help them protect their infants against infanticidal individuals (Palombit, Seyfarth & Cheney 1997). Females can also associate with each other to better protect their offspring against predators, male harassment or infanticidal conspecifics as shown in feral horses *Equus caballus*, bottlenose dolphins, crested macaques, yellow baboons *Papio cynocephalus* or chacma baboons *Papio ursinus* (Cameron, Setsaas & Linklater 2009; Frère 2010; Micheletta et al. 2012; Silk, Alberts & Altmann 2003; Silk et al. 2009).

Bonding with the right social partner

In the first two chapters of this dissertation, I similarly found that associations between female house mice in communal nests reduced maternal load and improved offspring survival. The success of such social bonds is likely to be determined by whether or not the individuals established an egalitarian and stable relationship.

In house mice, communal nests are only more likely to lead to beneficial outcomes for all parties when they are initiated between females that prefer each other. Otherwise, it results in aggression between females, and successful reproduction by only one or neither partner, as illustrated in an experimental study in indoor enclosures (Weidt, Hofmann & König 2008). In addition, field data from an open population of wild house mice revealed that reproductive females are selective, in that they associate in nests with a smaller number of females than non-reproductive females (Konig & Lindholm 2012). Moreover, females in this population do not initiate communal nests whenever there is an opportunity to do so, but are more likely to do so when there is a wide choice of partners available (Weidt, Lindholm & König 2014). Female house mice actively choose their nesting partner (Weidt et al. 2014) but the cues on which they base their choice remain unclear.

The house mouse is a plural breeder living in socially complex groups where breeding competition is high in males but also in females (König & Lindholm 2012; Rusu & Krackow 2004; Stockley & Bro-Jørgensen 2011). Consequently, even females who communally nest together may compete over reproduction (Weidt et al. 2008). As in any other cooperative interaction, cheating could occur between nesting partners (Ghoul, Griffin & West 2013; West, Griffin & Gardner 2007). For example, a female could improve her benefit to cost ratio

by contributing less than a fair share of maternal care than her partner or by being infanticidal to increase the ratio of own to total offspring in the communal nest. Previous studies in communally nesting mammals and birds have reported that the offspring of the first female to give birth, or lay eggs, in a communal nest is more susceptible to infanticide (Andersson & Eriksson 1982; Koenig et al. 1995; König 1994a; Vehrencamp, Koford & Bowen 1988). Moreover, communally nesting house mouse females showed some overlap in their stays at the nest suggesting that they may use this time to gain information on their partner's contribution to maternal care and prevent cheating (see Chapter 1). Choosing the right partner therefore has the potential to influence the risks of exploitation or conflict over reproduction (Rusu, König & Krackow 2004; Weidt et al. 2008).

Female house mice have been suggested to bond with each other according to their relatedness (Dobson, Jacquot & Baudoin 2000; Manning, Wakeland & Potts 1992). Although kinship does not prevent reproductive competition (Mumme, Koenig & Pitelka 1983), it provides indirect fitness benefits which may compensate for loss of direct benefits through competition (Hamilton 1964). Females, however, are not exclusively associated with kin. Previous studies in African elephants *Loxodonta africana* and sperm whales *Physeter macrocephalus* have reported examples of unrelated females sharing maternal care (Lee 1987; Whitehead 1996). Relatedness is not required for communal nesting to evolve as it conveys mutualistic fitness benefits (Bshary & Grutter 2002; Clutton-Brock 2002; König 1994a). Instead, females seem to prefer familiar over related unfamiliar females to initiate a communal nest (König 1994b). The same study reported that communal nests composed of familiar but unrelated females have a higher reproductive success than those composed of unfamiliar but related females. This may explain why communal nests are more likely to occur between females who show spatial proximity before breeding and also little aggression (Rusu et al. 2004; Weidt et al. 2008).

Success in raising offspring cooperatively may require behavioural complementarity between the nesting partners as suggested in pairs of cockatiels *Nymphicus hollandicus* where both parents cooperate over parental care (Spoon, Millam & Owings 2006). In this study, partners were defined as more behaviourally compatible when they showed greater proximity, synchrony, allopreening responsiveness and copulation frequencies and lower frequencies of aggression. A recent study in chimpanzees *Pan troglodytes* demonstrated that individuals prefer to socially bond with individuals of similar behavioural profiles (Massen & Koski 2014). The success of a cooperative task may therefore depend on the interaction between the behavioural profiles of the nesting partners. Studies examining the influence of exploratory

tendencies on reproductive success in great tits *Parus major* reported that assortative pairs for extreme exploratory tendencies fledged more chicks than disassortative pairs; however the opposite can be true when environmental conditions are harsher (Both et al. 2005; Dingemanse et al. 2004). As chapter 5 showed that female house mice can have different behavioural profiles, females may combine behavioural cues with other types of information when choosing their nesting partners. Chapter 2 emphasized that singly-sired litters were more common in communal nests than in solitary nests and were, for the majority of them, associated with litters sired by different males. The mixed paternity of these joint litters greatly improves offspring survival suggesting that females with the ability to gather information on the sexual partners of potential nesting partners could have a fitness advantage. The type of information required to determine the identities of the males with whom other females mated and how females use this information is totally unknown. House mice may rely on their particularly well developed sense of smell as females have already been shown to use males' scent markings to build a spatial map to locate males up to 14 days after encounter (Roberts et al. 2013).

Long-term consequences of an early social environment

Although individuals may benefit from social interactions, they may vary in their propensity to behave socially. Inter-individual differences in sociality can be genetically determined (Rushton et al. 1986) or be the result of epigenetic effects during the early development of an individual (Champagne 2010; Holmes et al. 2005). There is now increasing evidence that the early environment experienced by an individual can have strong consequences for its future behaviour (Champagne & Curley 2009; Hudson et al. 2011; Laviola & Terranova 1998; Levitsky & Barnes 1972; Lovic, Gonzalez & Fleming 2001; Mirescu, Peters & Gould 2004; Rödel & Von Holst 2009). In mammals, offspring fully depend on their mother until weaning so that maternal behaviour is the main source of epigenetic programming (Weaver et al. 2004). Accordingly, I found that differences between mothers were responsible for about 46% of the total variance in offspring weaning body mass in house mice (see chapter 3).

Offspring raised in communal nests interact with a larger number of carers, spend less time without a parent in the nest, have more surviving siblings than offspring raised in solitary nests, as well as a larger number of non-sibling familiar mice. Communal nests therefore represent a more social environment that can promote or favour the expression of social behaviours in offspring raised under such conditions (Benus & Röndigs 1996; Branchi et al. 2013; Curley et al. 2009; Hudson et al. 2011; Mendl & Paul 1991). Moreover, cross-fostering

studies found that offspring can inherit their parenting style from their foster parents (Champagne & Meaney 2001; Maestripieri et al. 2006). These behavioural inter-individual differences shaped during early development may not only affect individual's parenting style but may also influence their reproductive behaviour (Cameron et al. 2005; Champagne 2010) in addition to their network of familiar individuals. Whether or not communally raised female house mice will be more likely to raise their offspring communally has not yet been tested.

The influence of predispositions for social interactions may not be limited to females' nesting strategies but could also shape individuals' life history trajectories. Chapter 3 showed that mothers cannot improve their offspring lifetime fitness by increasing their level of maternal investment into offspring body mass. Although chapter 4 reported that adult body mass was a better predictor of individuals' lifetime fitness, several life history trajectories were apparent. This suggests that adult body mass may not be the only factor determining individuals' fitness. Reproduction in house mice is monopolized by the most competitive individuals able to get access to sexual mates for males (Andersson 1994; Oakeshott 1974) or nest boxes for females (Clutton-Brock 2009; Stockley & Bro-Jørgensen 2011). As dominance hierarchy is determined through the outcome of aggressive interactions between individuals, the biggest individuals are more likely to reach a higher fitness (Brown 1953; Clutton-Brock et al. 1988; Klemme, Ylönen & Eccard 2007). However, mice live in socially complex societies (König & Lindholm 2012; Perony et al. 2012) where small individuals may use their social competence to compensate for their physical disadvantage and become as successful as largest individuals. Chapter 5 provides an example of how particular sets of behavioural tendencies can contribute to improving the fitness of an individual. Similarly, sets of behavioural traits improving the outcome of social interactions are likely to be under selection pressures in social species. Through their decision to nest communally or their parenting style, females have two alternatives to maternal investment through which they can eventually tailor their offspring's lifetime fitness.

Conclusions and future research

Although communal nesting has already received a lot of attention, some aspects and potential benefits remain untested. The immunological consequences of allonursing have often been suggested as an adaptive hypothesis to the evolution of communal nesting but empirical evidence is still lacking (Boulinier & Staszewski 2008; Harris et al. 2006; Roulin & Heeb 1999). To date, most of the research on communal nesting has focused on its ultimate causes whereas its proximate mechanisms are still unclear. More particularly, social partner

choice has received far less attention than sexual mate choice (Bateson 1983; Dugatkin & Sih 1995). Similarly to sexual traits, social traits can evolve through natural selection (West-Eberhard 1983). Although studies of sexual mate choice explore individuals' preference for a variety of characters (Andersson 1994), most of the studies examining social associations between individuals primarily focus on kinship (Smith 2014). What criteria female house mice use to base their choice for a nesting partner, the likelihood and influence of cheating as well as the consistency of female associations are all topics that should stimulate further research.

The rather weak influence of an individual's body mass on its lifetime fitness suggests that other factors may play an important role in species living in complex social structure like the house mouse. Further studies may aim at developing reliable behavioural tests to assess individuals' social competence and test its influence on lifetime fitness. The large maternal influence on offspring development raises the question of whether females can tailor the future behaviour of their pups. Previous studies have reported that mothers can determine the morphology (Taborsky 2006) or the reproductive behaviour of their offspring (Cameron et al. 2005). A "predisposition" to nest communally in female house mice raised in communal nests, however, remained untested. A social competence continuum may explain why alternative life history trajectories are observed in males.

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I am of course very grateful to Anna Lindholm and Barbara König who both thought I was the best candidate to run this project. As I was only speaking "Fren-glish" at the time of my interview, I still wonder how I got the position… Although I want to believe they were deeply impressed by my scientific skills, I'm afraid I was only the funniest candidate they interviewed… In anyway, I prefer to ignore the reasons! Despite the eternity it took me to complete my PhD, I hope I nevertheless managed to turn their trust, time and money into a valuable scientific contribution.

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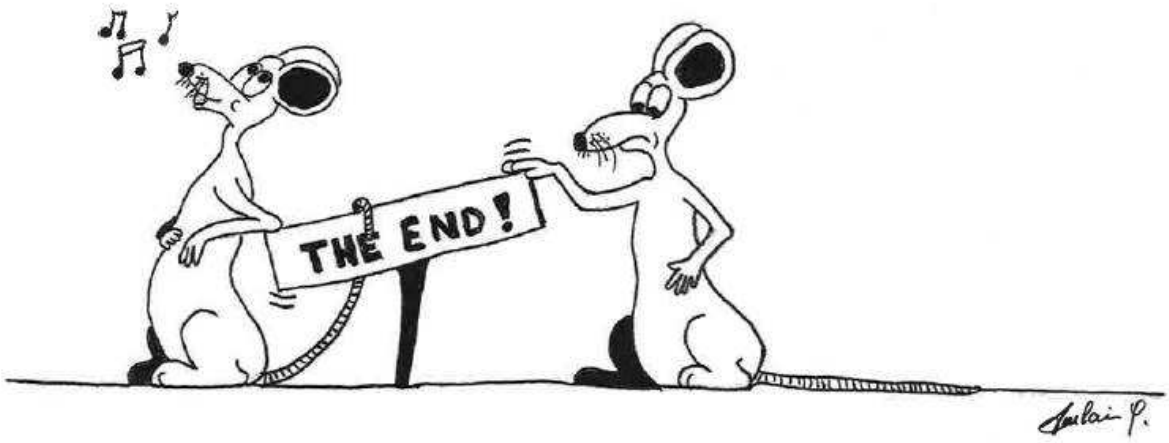
* Please, do not read as if I'm gonna do another one!



Personal details

Name: AUCLAIR
First name: Yannick
Birth date: 5th January 1982
Place of birth: Nevers (France)

Education

2001: **Baccalauréat Scientifique, Lycée Emilland Gauthey, Chalon-sur-Saône, France**

2005: **Bachelor in Biology "Biologie des Organismes", University of Burgundy, Dijon, France**

2007: **Master degree 1st year "Biologie des Organismes et des Populations", University of Burgundy, Dijon, France**

Thesis title: "Mate choice and evolution of partner preference in an avian monogamous species, the zebra finch *Taeniopygia guttata*"

Laboratory: Evolutionary Ecology group, Laboratoire Biogeosciences UMR-CNRS 5561, University of Burgundy, Dijon, France

Director: Prof. Frank Cézilly

2008: **Master degree 2nd year "Gènes, Sélection, Adaptation", University of Burgundy, Dijon, France**

Thesis title: "Does animal personality influence public information use by female zebra finches *Taeniopygia guttata* in a pairing context?"

Laboratory: Evolutionary Ecology group, Laboratoire Biogeosciences UMR-CNRS 5561, University of Burgundy, Dijon, France

Director: Prof. Frank Cézilly

2014: **Doctoral studies, University of Zurich, Switzerland**

Thesis title: "Short and long-term fitness consequences of maternal care in wild house mice *Mus musculus domesticus*"

Laboratory: Animal Behaviour group, Institute of Evolutionary Biology and Environmental Studies, University of Zurich, Switzerland

Directors: Dr. Anna K. Lindholm and Prof. Barbara König

Lab accreditation

Accreditation in laboratory animal science: **Study director FELASA-Category C**

Awards

2007: **Master Scholarship** from the "Conseil Régional de Bourgogne" – 4 244€

2011: **Best poster prize** Ethoges meeting "Cooperation and conflict", Zurich, Switzerland

Auclair Y., König B. & Lindholm A. K. Socially mediated polyandry: a new benefit of communal nesting in mammals. *Behavioral Ecology*, Accepted.

Auclair Y., König B., Ferrari M., Perony N. & Lindholm A. K. 2014. Nest attendance of lactating females in a wild house mouse population (*Mus musculus domesticus*): benefits associated with communal nesting. *Animal Behaviour*, 92, 143-149.

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Transferable skills

Scientific writing course	1 ECTS
Scientific writing: Journal club with a difference	1 ECTS
Contemporary analysis for ecology	No ECTS for PhD students
Statistics for free: Generalized linear models in R	2 ECTS
Statistics for free: Mixed-effect models in R	1.5 ECTS
Good graphics using R	1 ECTS

Evolutionary Biology

BIO 554 Topics in Evolutionary Biology	1 ECTS
BIO 620 Literature Seminar "Animal Behaviour"	1 ECTS
BIO 608 Literature Seminar "Ecology and Evolution"	1 ECTS

Professional meetings

Poster: 13th meeting of the International Society for Behavioral Ecology Perth, Australia	1 ECTS
Oral: 14th meeting of the International Society for Behavioral Ecology Lund, Sweden	1 ECTS
Annual Research Symposium of the PhD program	Compulsory

Other

Introductory course in laboratory animal science	2 ECTS
Workshop "Evolutionary Genetic Approaches to study social evolution" University of Copenhagen, Denmark	5 ECTS
Workshop "Social evolution: from theory to data (and back again)" University of Neuchâtel, Switzerland	1 ECTS
Workshop "Maternal effects: underlying mechanisms and implications for life history evolution" University of Bern, Switzerland	2 ECTS
ECO 391 Postdoc funding and career management	1 ECTS

Total: 22.5 ECTS